Ecological Studies 210

Wolfgang J. Junk, Maria T.F. Piedade
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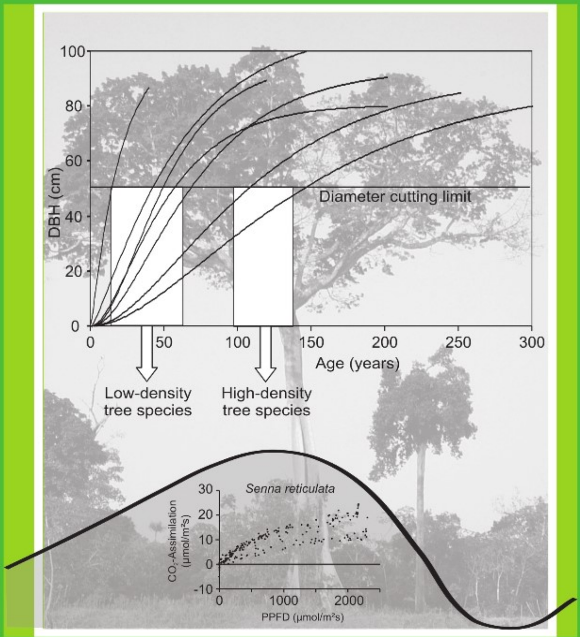
Editors

Amazonian Floodplain Forests

Ecophysiology, Biodiversity and Sustainable Management



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Amazonian Floodplain Forests

Ecophysiology, Biodiversity and Sustainable Management

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Upper figure: Figure 21.4 this volume. Mean cumulative diameter growth curves of 12 low-density and high-density timber species from the Central Amazonian várzea floodplain forests. Figure by Jochen Schöngart.
Lower Figure: Figure 10.1 this volume. Measured data points during 15 months of recording. Figure by Pia Parolin with permission from the authors.

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Foreword

In 1989, growing concern about the destruction of tropical ecosystems and the need to improve the living conditions of local populations in Amazonia and the *cerrado* led Brazilian and German politicians and scientists, during the annual meeting of the Joint Commission, to expand and intensify the already existing bilateral cooperation in the field of ecology. The efforts aimed to achieve the following common interests: (1) develop concepts for the sustainable use and protection of tropical ecosystems, (2) solve or diminish already existing environmental problems, (3) consolidate or expand already existing facilities for developing tropical ecology research, and (4) promote scientific collaboration through joint research projects and training.

The partners selected the following geographic regions and research projects: (1) the forests and floodplains in the Amazon basin, (2) the forests of the coastal region (Mata Atlântica) and its inland waters, and (3) the floodplain of the upper Paraguay River (Pantanal) and its catchment area.

The resulting program, entitled Studies of Human Impact on Forests and Floodplains in the Tropics (SHIFT), became established within the framework of the special agreement on cooperation in the field of environmental research and technology between the Instituto Brasileiro do Meio Ambiente e Recursos Renováveis (IBAMA) and the Deutsche Forschungs- und Versuchsanstalt für Luft- und Raumfahrt e.V. (DLR). In 1992, the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) took the position of leadership of the Brazilian side, participating in the project's financing.

In light of the multiplicity of factors contributing to the impact of the study biomes, including those of anthropogenic origin, the different levels of available knowledge, infrastructure, and human resources, and the need for urgent actions, the SHIFT Program, from its beginning, opted for a highly pragmatic approach. It aimed at: (1) a description of the dimensions of human impact, (2) an analysis of the reasons underlying these anthropogenic effects, (3) the elaboration of proposals to mitigate the negative side effects of human action, and (4) the development of new methods for sustainable management, taking into consideration the specific ecological, economical, social, cultural and political conditions of the individual study biomes and ecosystems.

To reach these goals, multidisciplinary and interdisciplinary studies and a multi-institutional approach were recommended, in a combination of investigations into terrestrial ecology, limnology, agriculture, forestry, fishery, animal husbandry, soil science, climatology, and environmental technologies, as well as socio-economy, regional planning, and resource management.

Logistic and scientific basis for the research projects in the Amazon River floodplains was the successful cooperation between the National Institute for Amazon Research (INPA) in Manaus, and the Max-Planck Institute for Limnology (MPIL), Plön that was established in 1962 by Prof. Djalma Batista and Prof. Harald Sioli. The new projects were realized under the coordination of Dr. Maria Teresa Fernandez Piedade of INPA and Prof. Dr. Wolfgang Junk, head of the Working Group of Tropical Ecology at MPIL. INPA provided laboratory space, and BMBF, CNPq, and MPIL improved the projects' infrastructure with equipment, financed scholarships, travel expenses, and consumables of the projects. The scientific results have been published in more than 600 scientific articles, book chapters, and reports. Numerous Ph.D., M.Sc. and Bachelor theses were written by students involved in the program. In 2000, the first book was published (Junk, W.J., Ohly, J.J., Piedade, M.T.F., and Soares, M.G.M., (eds): The Central Amazon Floodplain: Actual Use and Options for a Sustainable Management. Backhuys Publishers, Leiden: 584pp). The analyses of the already published material showed big gaps in the knowledge of ecophysiology, biodiversity and sustainable management of the floodplain forest, and since 1997 the field work concentrated on this subject.

In 2002, an independent joint scientific commission analyzed the program and recommended its continuation for three more years in order to finalize the projects and elaborate praxis-oriented solutions. However, a change in both the Brazilian and the German political leadership led to the abrupt end of SHIFT, placing at risk the many fruits of this successful cooperation. With the support of their institutions, a strong will and even personal resources, the program's leading scientists managed to continue the work, even though on a much smaller scale, thus avoiding major losses of scientific results, infrastructure, and human resources.

In August 2003, a cooperation contract with the Mamirauá Institute for Sustainable Development was signed. In 2005, the research project in the Mamirauá Reserve was selected as a Demonstration Project of UNESCO's Ecohydrology Programm (IHP). In 2006 the research group initiated a project financed by the CNPq to support "research to develop a sustainable community-based management of floodplain forests in the Amanã and Mamirauá Reserves". In 2007, the team received funding of a project in the Brazilian research initiative "Nucleus of Excellence Projects" (PRONEX), supported by CNPq and Amazonas State Science Foundation (FAPEAM). The main goal of this project is to typify the wetlands of the Amazonas State, only possible owing to the accumulated information of the team during the past decades. Other two projects were approved in 2008 by CNPq, supporting studies on the impact of climate change on species shifts and diversity losses of Amazonian floodplain vegetation.

The increasing drive in wetland research in South America culminated with the realization of the eighth INTECOL Wetland Conference in 2007 in Cuiabá, Brasil, and led to the elaboration of this book. It summarizes the major findings of the SHIFT Program and reviews the recent results of research activities about floodplain forests in Central Amazonia regarding distribution, ecology, primary production, ecophysiology, typology, biodiversity and use. Importantly, it offers recommendations for sustainable management and future projects in science and development of the Amazon floodplain forests.

This is the first integrative book on the functioning and ecologically oriented use of floodplain forests in the tropics and sub-tropics. It provides a solid scientific basis for wetland ecologists, foresters, environmentalists, and wetland managers. It is also an excellent textbook for students working in Amazonian floodplain forests and similar forest types in other regions. The authors have worked for many years in the Amazon basin and have a profound knowledge of the subject. They interpret their findings under an integrating scientific concept, the Flood Pulse Concept.

On behalf of the coordinators of the research projects and the coeditors of this book I gratefully acknowledge the financial support of the CNPq, BMBF, Max-Planck-Society and Amazonas State University (UEA), and the infrastructure provided by INPA, MPIL and Mamirauá Reserve especially Dr. José Márcio C. Ayres (in memoriam), and Helder Lima de Queiroz. We gratefully acknowledge the support of Prof. Dr. José Galicia Tundisi, president of CNPq from February 1995 until December of 1998, and his collaborators Dr. Carlos Roberto de Faria e Souza, Dr. Glauter Pinto de Souza and Dr. Gilvan Marcelino. Our special thanks go to Ms. Izaura Matiko Yamada, analyst in science and technology of CNPq, who gave substantial help in all bureaucratic aspects. On the German side we gratefully acknowledge the help of Dr. Günther Keil from BMBF, Dr. Emil Stüttgen from KFA Jülich, Dr. Helmut Bianchi from GKSS Geesthacht, and Dr. Klaus Matthes, from 1990 to 1995 scientific attaché of the German Ambassy in Brasilia. Our special thanks go to our technicians and field workers, mainly Celso Rabelo Costa, Valdeney de A. Azevedo, Conceição Lúcia Maia Costa, Edivaldo de Souza Ferreira, Wallace Rabelo Costa, Agenor Negrão da Silva, and Mario Picanço in Manaus, Jackson de Castro and Emilson José Pereira Tiburcio in the Mamirauá Reserve, and Uwe Thein (in memoriam), Stephanie Barthel, Elke Bustorf, Berit Hansen, Gerda Lemke and Sabine Meier in Plön. Without their knowledge, field and laboratory experience and enthusiasm, these studies would not have been performed at this high level.

Plön, Germany, spring 2009 Wolfgang J. Junk

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Part I

Amazonian Floodplain Forests and the Environment

Chapter 1
An Introduction to South American Wetland Forests: Distribution, Definitions and General Characterization

Wolfgang J. Junk and Maria T.F. Piedade

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Abstract This chapter provides an introduction to the ecology of wetland forests, their ecophysiology, distribution, species diversity, classification and use, with emphasis on Amazonia. Wetland forests occur in all continents and all regions except in deserts, high altitudes, and high latitudes. Their importance for humans and the environment is often underestimated because in developed or densely colonized regions such as Europe, North America, Australia, and the Indian subcontinent, many of them have already been destroyed or strongly modified. In other regions, such as Siberia, the Zaire River basin and the Amazon River basin they still

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cover large areas; however, scientists and politicians have placed little emphasis on their study and protection, or on developing sustainable management practices. In this chapter, we describe the general terminology for wetland forests and provide a classification of Amazonian wetland forests. We discuss the distribution of major wetland forests in South America and the impact of hydrology and nutrient status of water and soils. Distribution, species diversity, and the level of adaptation of trees of wetland forests is the result of long periods of evolution, without major extinction episodes. These conditions prevailed for many millions of years in the Amazon basin as shown by paleo-climatic and paleo-botanical evidence, leading to the development of the most species rich and highly adapted floodplain forest on the globe. In light of this history, we give examples for specific adaptations and survival strategies. Finally, Amazonian wetlands have been colonized by humans since their arrival on the sub-continent, about 12,000 years BP. More recently, European immigrants have used the wetlands for fishing, subsistence agriculture, timber exploitation and increasingly for cattle and water-buffalo ranching. Large scale ranching activities are especially detrimental for the forested Amazonian wetlands, because ranchers destroy wetland forests to increase the area of natural and planted pastures. This is also detrimental for forestry, fisheries, and the maintenance of biodiversity.

1.1 Introduction

Formerly, wetland forests were common in most parts of the continents, except in deserts, high latitudes, and high altitudes. Human hunters and gatherers quickly discovered that wetlands provided water, game animals, and protection and used them despite their negative aspects, such as insect nuisance and flooding. When humans became sessile, they recognized the great potential of river floodplains for agriculture and ranching because of their fertile soils. This was especially true for large tropical river floodplains with a predictable flood pulse. Accordingly, high cultures developed, for instance, along the Euphrates and Tigris Rivers in Mesopotamia, the Ganges, and Brahmaputra Rivers in India, and along the Nile River in Egypt. In the floodplain of the lower Amazon River, traces of human colonization date back about 12,000 years BP (Roosevelt 1999). Humans adjusted their management methods to natural flood cycles and were able to benefit from them.

In temperate regions, unpredictable floods initially hindered colonization of the floodplains. However, with increasing technical knowledge, dike construction improved and floodplains became increasingly used for traditional upland agriculture or for cattle ranching during low-water periods. These activities and the increasing demand for wood resulted in an accelerated destruction of floodplain forests in nearly all countries. The demand for arable land to accommodate an increasing population also led to the drainage of swamps and the destruction of swamp forests. Today, wetland forests belong to the most threatened forest types worldwide. Human pressure on remaining forest plots is rising directly due to logging for timber and firewood, agriculture, pasture formation, housing and infrastructure construction, or indirectly due to hydrological changes, such as water abstraction, diking, and flooding by reservoir construction, all of which negatively impact forest habitats.

These activities are not limited to densely populated areas but also increasingly affect wetlands in remote areas (Junk 2002). The Amazon River basin harbors a human population of about 25 million people, of which about 70% live in urban centers. The human population density in large areas is <0.5 person per square kilometer. Despite this low density, the floodplain forests along the large Amazonian Rivers are becoming severely affected by logging and by transformation to crop land and pasture for cattle ranching (Goulding et al. 1996; Ohly 2000a,b; Junk and Piedade 2005).

Scientific research on Amazonian wetlands started at the beginning of the last century (summarized in Junk and Piedade 2004). Botanists were fascinated by the species-rich forests able to survive floods up to 10 m deep for as long as up to 8 months per year. The first floristic studies were carried out by Spruce (1908), Huber (1910), and Ducke (1913), and later by Ducke (1949), Ducke and Black (1953), Rodrigues (1961), and Takeuchi (1962), among others. These studies revealed different forest types and identified flooding, the nutrient status of water and sediments, and phytogeography as factors influencing the diversity of species composition and distribution.

At the beginning of the 1970s, the Brazilian government initiated major efforts to link the economically underdeveloped Amazon basin to the industrialized southern region of the country. Large projects for the construction of highways and airports, hydroelectric energy production, mining, petrol exploitation, agriculture, cattle ranching, and timber exploitation, and the establishment of a free-trade zone at Manaus stimulated a scale of development that could not be accompanied or controlled adequately by administrative or legislative measures and, even less, guided by scientific research. Research concentrated mostly on priorities financed by the government and was thus forced to ignore other important fields. Negative consequences of the development projects on the wetlands and their resources, especially floodplain forests, were thus inevitable.

The valiant efforts of a Brazilian scientist, Dr. Marcio Ayres, resulted in the targeting of floodplains for environmental protection. In 1983, Ayres, who was a doctoral student at the time, went to the Mamirauá region, near Tefé, to study the white-uacari monkey (*Cacajao calvus calvus*), which is endemic to that area. He wrote an excellent thesis on the monkey and its habitat, the floodplain forest of Mamirauá (Ayres 1986, 1993). Moreover, he also alerted the Brazilian Environmental Agency and the government of the State of Amazonas to the need to protect the area. This resulted in the establishment, in 1990, of the first Sustainable Management Reserve in Amazonia. Currently, the reserve protects about 1,124 million hectares of floodplain area most of it covered by near-pristine floodplain forest. This area constitutes an important platform for basic and applied research on different aspects of the central Amazonian floodplains and provides opportunities to practically test management options (Queiroz and Peralta 2010).

Along with many individual researchers, two teams realized long-term studies on Amazonian floodplain forests. At the beginning of the 1960s, Professor Harald

Sioli and co-workers together with scientists at the Instituto Nacional de Pesquisas da Amazonia (INPA) started ecological research on the Amazon floodplain near Manaus. Junk (1980) was the first to point out the flood pulse as the driving force in river floodplain systems and later published, with his colleagues Bayley and Sparks, the Flood Pulse Concept, which became an internationally recognized analysis of the processes in large-river floodplains (Junk et al. 1989). Research on the floodplain forest began in the 1980s (Worbes 1983) and was intensified in the mid-1990s with the financial assistance of the Brazilian Research Council (CNPq) and the German Ministry of Science and Technology (BMBF). The results of these studies are presented in the chapters of this book.

In the Peruvian pre-Andean Amazon basin, scientists from the University of Turku, Finland, started investigations in the early 1980s, in cooperation with several Peruvian institutions (Oficina Nacional de Evaluación de Recursos Naturales, ONERN, Instituto Nacional Geologico, Mineralogico y Metallurgico, INGEMMET, Universidad Nacional de la Amazonia Peruana, UNAP, and others). The team concentrated on floristic studies, the description and mapping of forest types on floodplains and upland, and on relating these types to river dynamics and soil quality. It highlighted the importance of river activity and geologic dynamics in the pre-Andean region for plant species diversity in Amazonia (Kalliola et al. 1993).

In the following sections, we discuss the terminology used for wetland forests in general and for Amazonian wetland forests specifically. We review the actual distribution of wetlands in South America and the environmental factors affecting them. General information is provided on the evolution of Amazonian floodplain forests, the different types are characterized, and the various classification systems are discussed. We also describe the general strategies employed by trees to survive periodic flooding and the use of field measurements by researchers to estimate flood tolerance. Finally, services provided by floodplain forests to humans are discussed.

1.2 Terminology of Wetland Forests

The English scientific literature uses the general term "riparian forests" for wetland forest communities along rivers and lakes. There are many definitions of riparian wetlands. Hydrologically, they are defined as "lowland terrestrial ecotones which derive their high water tables and alluvial soils from drainage and erosion of adjacent uplands on the one side or from periodic flooding from aquatic ecosystems on the other" (McCormick 1979). A functional definition states that "riparian areas are three-dimensional ecotones of interaction that include terrestrial and aquatic ecosystems, that extend down to the ground water, up above the canopy, outward across the floodplain, up the near-slopes that drain to the water, laterally into the terrestrial ecosystem, and along the water course at a variable width" (Ilhardt et al. 2000).

Both definitions point to the ecotonal character of riparian wetlands between water bodies on the one side and the upland on the other. At their smallest scale, riparian wetlands can be the immediate water's edge – where some aquatic plants and animals form a distinct community – that becomes periodically flooded over areas of a few tens of meters in width. At medium scale, these wetlands comprise bands of vegetation, while at the largest scale they form extended floodplains, tens of kilometers in width, along large rivers. In the latter case, the complexity of the riparian wetlands increases to the extent that many scientists confer upon them the status of specific ecosystems (Junk 1980; Odum 1981; Mitsch and Gosselink 2000).

Riparian zones are covered by different plant communities, including different types of wetland forests. When riparian forests become extended, e.g., in floodplains along large rivers, such as the Mississippi River, the term “bottomland hardwood forest” is often used. The term “gallery forest” is frequently applied to riparian forests along water bodies in un-forested landscapes. Forests growing in swamp habitats with relatively stable water levels and long-lasting flood cycles are called swamp forests. These are dominated by a few highly flood-resistant species, such as the Bald Cypress (*Taxodium distichum*) and Water Tupelo (*Nyssa aquatica*) in North America, and palm trees in South America (*Mauritia* spp., *Astrocaryum* spp., and *Bactris* spp.). Forests in brackish water are called mangrove forests.

Here, we use the term “wetland forests” to refer to all types of forests subject to irregular, seasonal, or long-term flooding. “Floodplain forest” is used for all types of forests subject to periodic flooding by freshwater, and “swamp forest” for all types of forests subject to long-lasting flooding or waterlogging of the soil with freshwater. The term “riparian forest” is reserved for narrow forest strips along water bodies in forested and unforested landscapes, e.g., savannah areas (Rodrigues 2000).

Every region has local names that describe the different types of wetland forests. These names may provide insight into the type of flooding regime and the nutrient status of the system, or indicate dominant tree species. But local names are often used differently in different regions and therefore must be defined when used in the scientific literature. This is later shown for the terms *várzea* forest and *igapó* forest, which are used to describe the floodplain forest types that we studied in Central Amazonia. Non-wetland forests on the upland (*terra firme*) are called *terra firme* forests.

1.3 Occurrence of Wetland Forests in South America

Wetland forests occur all over South America because of the large number and vast extension of wetlands. A vegetation map of South America (Eva et al. 2002) based on multi-resolution satellite data indicated the areas listed in Table 1.1.

However, these numbers no doubt strongly underestimate the extent of wetlands, since only large wetlands were mapped and the definition of vegetation types remains biased in favor of terrestrial types that are better known. Junk (1993), using RADAM/BRASIL maps and botanical data on plant communities, estimated that 20–25% of Amazonia is periodically flooded. For all of South America, this number should amount to at least 15%, i.e., about three times the area indicated by Eva et al. (2002). The data reported by Melak and Hess (2010) confirmed the estimates of Junk (1993).

Table 1.1 Extent of wetlands and water bodies of South America (Eva et al. 2002)

Type of wetland	Extent (km^2)	Locality
Mangrove forests	17,290	East coast, from Orinoco delta down to Salvador West coast, down to Tumbes in Peru
Freshwater flooded forests	199,281	Along large Amazonian Rivers, Orinoco upper reaches of Rupununi and Mazaruni, coastal flooded forests from the delta of the Orinoco to the Maroni River, northern Amapá to the mouth of the Amazon River (west of the island of Marajó)
Swamp forests, open with palms	53,907	In Peru, the Pastaza fan; in Brazil, Amapá coast, western part of Marajó, and courses of the Guaporé River
Flooded savannah	320,941	Llanos of Venzuela/Colombia, northern parts of Rio Atrato and Rio Magdalena in Colombia, Campos de várzea along the Amazon River and its tributaries, Ilha do Bananal, Pantanal do Mato Grosso, parts of the Llanos of Moxos, west bank of Paraguay River, wet chaco, lower reaches of the La Plata River, south of the confluence of the Paraná and Paraguay Rivers
Flooded shrublands	12,957	Region north of the Rio Negro and along the Rio Branco in Roraima
Moorelands/heath	106,896	Mosaic of bogs, herbaceous and shrub vegetation in the humid temperate region in southern Chile and Argentina
Salt pans	9,409	Altiplano
Water bodies (natural & artificial)	220,219	
Total	940,900	

About half of the wetland area of Amazonia is covered by woody vegetation (Klinge et al. 1990). Hueck (1966) summarized what was known at the time about the ecology, species composition, and importance of the forests in South America. That study noted different wetland forests along the large South American rivers as well as rainwater-fed wetlands.

Most of the dense wetland forests are concentrated in the domain of the Amazon rain forest. They cover extended areas along the lower courses of all large Amazonian rivers (Klinge et al. 1990; Junk 1993) and the rivers of the southern Orinoco basin (Godoy et al. 1999; Rosales et al. 2001, 2002). Narrow strips of riparian forests also occur along all lowland rain forest streams. Large forested areas exist on insufficiently drained, periodically flooded white sand areas at the upper Negro and Orinoco River (Bana and Caatinga woodlands, Klinge et al. 1977; Klinge 1978b; Klinge and Medina 1979; Bongers et al. 1985). Prolonged flooding leads to species-poor *Mauritia flexuosa* palm swamps, e.g., north and south of the Negro River, upriver of the city of Barcelos, in the Amazon and Orinoco deltas, and in the pre-Andean zone. They are nutrient-poor and characterized by a small flood amplitude. In Brazil, they are called *buritizal*, in Peru *aguajal*, and in Venezuela *morichal*. In Bolivia, southern Peru, and southwestern Brazilian Amazonia, there are bamboo swamp forests, which in Brazil are called *tabocal*.

Comprehensive studies on the geology, geomorphology, and vegetation cover of the pre-Andean zone showed a complex mosaic of habitats as a result of river activities; 26.6% of the lowland forests showed characteristics of recent erosional and depositional activity; 12% of the area comprised floodplains, and 14.6% previous floodplains with a mosaic of abandoned river beds, oxbows, and sedimentary beds of different age. These findings point to the overwhelming importance of rivers in structuring western Amazonia in recent history (Salo et al. 1986). Floristic studies identified floodplain forests of different species composition that are the result of recent river activity, different flooding regimes, or different water and soil qualities. The authors postulated that forest disturbances due to modern and previous river dynamics were partially responsible for the high biological diversity of the upper Amazon basin, and that the number of species confined to floodplain or denuded-soil forests is exceptionally high in the Amazon. Certainly, the close connectivity of upland forests and habitats to different flooding regime has favored the development of flood-resistant ecotypes of upland species (Kalliola et al. 1993).

Extended forests occur also in the large floodplain along the lower Paraguay-La Plata River. Large parts of the floodplain forests along the upper and middle Parana River have been destroyed because of the construction of hydroelectric power plants, which now occupy large areas of the former floodplain. Remnants can still be found in the 250-km-long stretch between the Porto Primavera Dam and the Itaipu Reservoir (Thomaz et al. 2004).

Large wetlands are found in savanna areas, such as the Pantanal at the upper Paraguay River, the Bananal at the Araguaia River, the Moxos Savannas at the Madre de Dios, Beni, Mamoré, and Guaporé Rivers in Bolivia, the Roraima and Rupununi Savannas in northern Brazil and the Guianas, and the Llanos of Venezuela. They are partially covered by different types of flood-tolerant forests and strips of riparian forests along river courses as well as around lakes, and savannah vegetation that at high water comprises many aquatic macrophytes (Junk 1983). Swamps along the headwaters of Brazilian cerrado streams covered mostly by sedges, grasses, herbaceous plants, and a few shrubs and trees are called *veredas*.

Permanent wet depressions are covered by palm swamps (*Mauritia flexuosa*). Along the courses of all rivers in the savanna, cerrado, and chaco areas, there are species-rich gallery forests. These forests occupy the ecotone between the dry upland and the river channel and form important forested corridors in the landscape that allow the migration of animals between isolated forest plots. They also represent important refuges for upland tree species that occur along their edges (Kellman et al. 1994; Meave and Kellman 1994; Meave et al. 1991).

Along the Atlantic Ocean coast, mangroves begin to grow in small patches from about 28°S to Central America, forming major forests near São Luis (5°S), in the Amazon River Delta, the Orinoco River Delta, and the Magdalena River Delta. At the coast of the Pacific Ocean, mangroves occur only in small patches and extend southerly only down to the Gulf of Guayaquil (5°S) (Lacerda et al. 2002).

1.4 The Impact of Hydrology on South American Wetlands

The conceptual basis to explain the importance of the length, depth, frequency, shape, and predictability of inundation on large-river floodplains in general was elaborated by Junk et al. (1989) in their Flood Pulse Concept (FPC), which describes the structures and processes in large-river floodplains. The FPC states that the flood pulse is the driving force in floodplain systems. It controls both the occurrence and the distribution of plants and animals, determines life-history traits, affects primary and secondary production, and influences decomposition and nutrient cycles in water and soils. The predictability of the flood pulse facilitates the adaptation of organisms to the change between aquatic and terrestrial phases, increasing their ability to efficiently make use of periodically available resources. In temperate regions the light/temperature (summer/winter) pulse, and in semiarid regions the precipitation (dry/rainy season) pulse may overlap with the flood pulse, obscuring the impact of the latter. For further discussions of the FPC, see Junk and Wantzen (2004) and Junk (2005).

Large Amazonian rivers integrate the individual precipitation events of large catchments, which, in turn, are influenced by pronounced dry and rainy seasons and by the snow melt in the Andes. Therefore, these rivers show long-lasting, predictable flood pulses of high amplitude (Fig. 1.1). The ecology of the Central Amazon River floodplain has been well-studied, for example, in Sioli (1984a,b), Junk (1997a), and Junk et al. (2000a). These studies described a predictable arrangement of plant communities that is controlled not only by the inundation stress of the flood pulse but also by hydrologic disturbances that may reset these communities to earlier seral stages.

Low-order rivers are influenced by individual heavy rainstorms and show a spiky, unpredictable flood pattern of short floods that increase in frequency and in baseline flow during the rainy season (Fig. 1.2). Forests along streams and rivers play an important role by mitigating floods, trapping sediments, increasing bank stability, stripping nutrients from water and sediment, and providing food and habitat for animals and raw material for organic soils. They also filter nutrient input from the upland, enhance denitrification, equilibrate temperature, and control in-stream primary production by shading. Due to their linear arrangement, riparian forests are important corridors for genetic exchange between remote populations of aquatic and terrestrial organisms, mainly in unforested landscapes. Tree species diversity is high but species lists are rare, and the ecology of these wetlands has been poorly studied (Wantzen 2003; Wantzen et al. 2007). The small lateral extensions of these wetlands have resulted in a dramatic underestimation of the total area covered by them. Riparian forests along streams and low-order rivers in the rain forest are mapped as upland forests (*terra firme* forests). Junk (1993) estimated that, in Amazonia, they cover an area of about 1 million square kilometers. This corresponds to about 50% of the entire wetland area of the basin.

Because of the flat relief, drainage in large parts of the South American lowlands and plateaus is insufficient and leads to flooding due to excess rainfall. Periodic

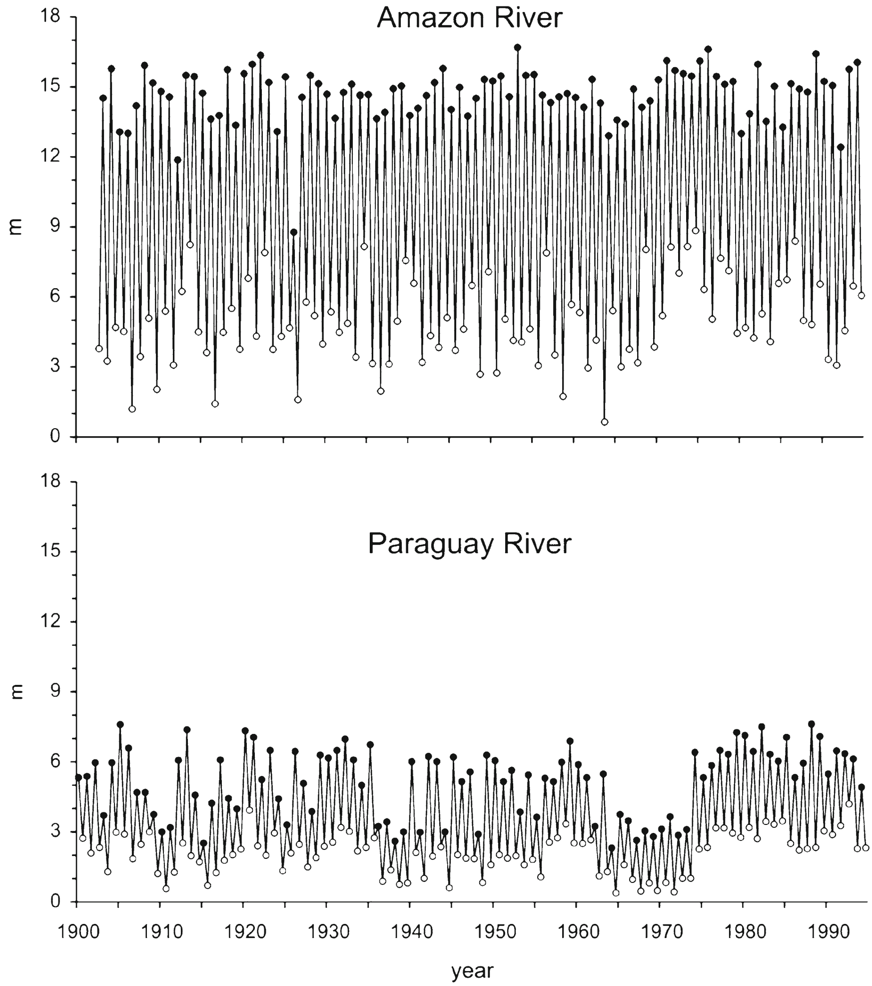

Fig. 1.1 Water-level fluctuations of the Negro/Amazon River at Manaus and the Paraguay River at Ladario (Data of the Amazon River from the Manaus harbor authority, of the Paraguay River from the Departamento Nacional de Águas e Energia Elétrica). ● = maxima; ○ = minima

flooding and waterlogging of the soils during the rainy season has been reported from the Bana and Caatinga woodlands at the upper Negro and Orinoco Rivers, the Brazilian and Bolivian cerrado, the Argentinean chaco, and the Venezuelan savannah. These areas drain slowly to connected rivers. Isolated shallow lakes remain in depressions but can completely dry out during extreme dry periods. These floodplains show a long-lasting, predictable flood pulse of low amplitude (Fig. 1.3). In savannah areas, drought stress during the dry period can be intense. Nunes da Cunha and Junk (1999) reported that many tree species in the Pantanal of

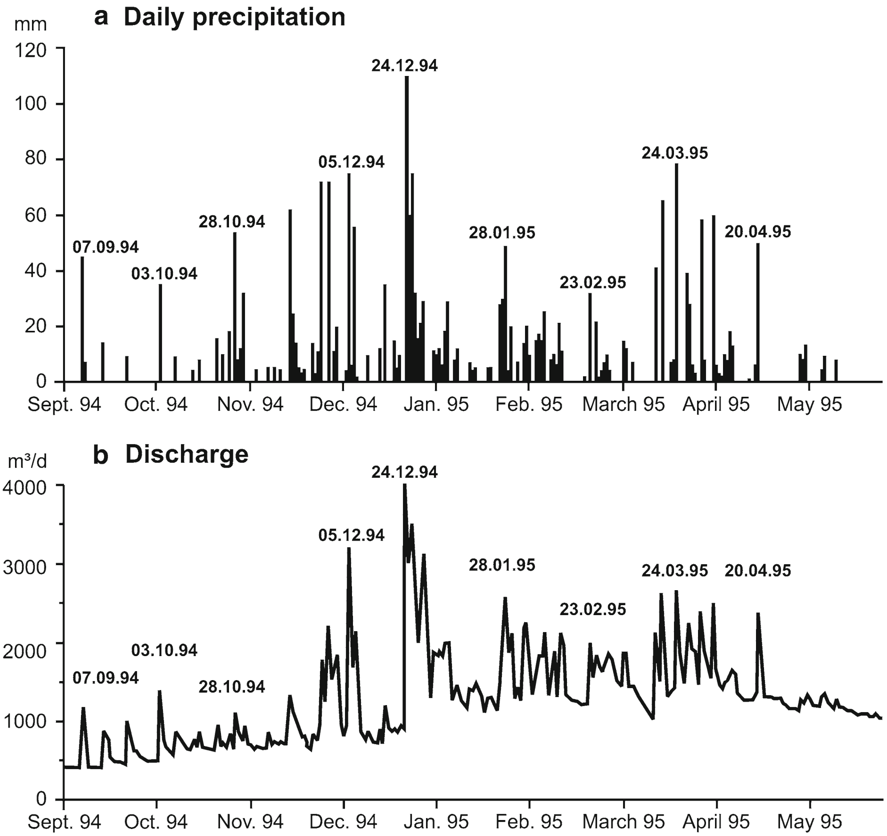

Fig. 1.2 Precipitation and discharge of the Tenente Amaral, at the study area a second order cerrado stream in Mato Grosso near Cuiabá (according to Wantzen 2003)

Poconé, upper Paraguay basin, are highly tolerant of drought and flood stress and that multi-annual periods of heavy drought and wild fires control the distribution of flood-adapted tree species, such as *Vochysia divergens*. Ishima (1998) showed that the increment in the diameter of *Vochysia divergens* is positively correlated with precipitation and restricted by drought stress but not by flood stress. Similar environmental conditions exist in the vast flooded savannas on Ilha do Bananal at the Tocantins River, in the Llanos dos Moxos at the Madre de Dios, Beni, Mamoré and Guaporé Rivers, in the flooded savannas of Roraima and Rupununi, and in the Llanos of Venezuela.

In the estuary, the tides impose a predictable polymodal flood pulse, with a moderate-amplitude effect on that of the Amazon River. This flood pulse affects the mangrove ecosystem but upriver also fresh water habitats. However, there have been no studies on the respective consequences.

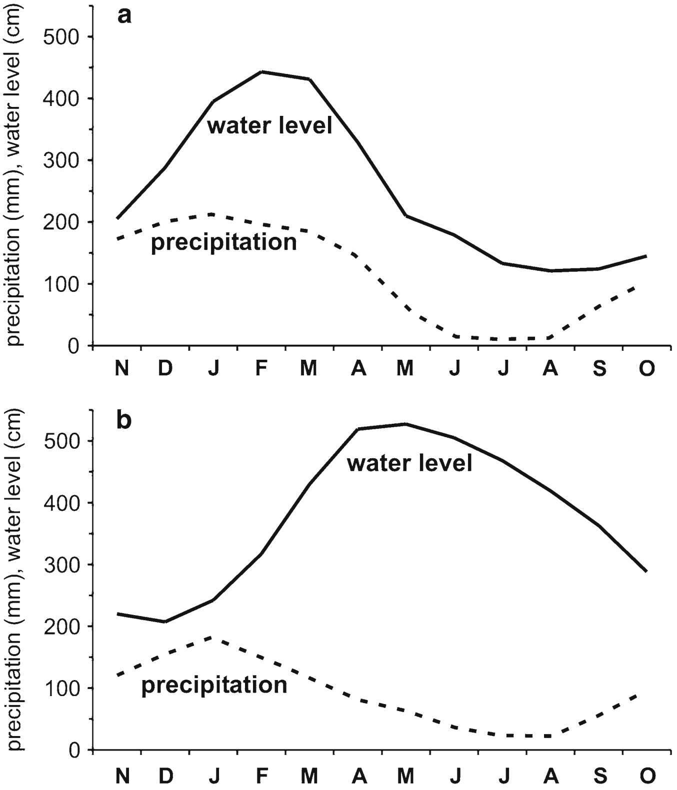

Fig. 1.3 (**a**) Mean monthly precipitation near Cuiabá (1933–1993) and mean water-level of the Cuiabá River at Cuiabá (1971–1988), northern Pantanal (According to Zeilhofer 1996). (**b**) Mean monthly precipitation near Corumbá (1912–1971) and mean water level of the Paraguay River at Ladário (1979–1987), southern Pantanal (According to Hamilton et al. 1999)

1.5 Geology and Paleoclimatology of Amazonia and the Evolution of Wetland Forests

The geologic and paleoclimatic history of Amazonia is closely related to water. The Amazon Basin is part of a very old depression that already existed in the Gondwana continent and then opened to the west. When South America separated from Africa, during the Early Cretaceous period, about 110 million years (Ma) before present (BP), the basin was already closed in the west by the Early Andes, except for an opening to the Pacific (Marañon Portal or Guayaquil Gap) that closed probably during the Late Cretaceous period (73 Ma). Rivers drained to the west into a depression along the eastern border of the Early Andes that opened to the Caribbean Sea. With the uplift of the Andes, the pre-Andean depression was subjected to marine ingressions in the Late Cretaceous (83–67 Ma), the Early Tertiary (61–60 Ma), and the Late Tertiary (11.8–10 Ma) periods, as indicated by marine sediments. Following the interruption of marine transgressions, the depression became covered by rivers, lakes, and extended wetlands. Large freshwater lakes were formed in the Tertiary period (Lago Pozo in the middle Eocene–early Oligocene, 43–30 Ma; and Lago Pebas in the Late Tertiary, 20–11.8 Ma) and were filled with sediments of riverine origin from the Andes and the shields of Central Brazil and the Guianas. In the Late Miocene (8 Ma), the connection to the Caribbean Sea and the Orinoco basin was closed by the Vaupes Arch. The Amazon River opened its way to the Atlantic Ocean by breaching the Purus Arch, and the modern Amazon drainage system incised large valleys and floodplains in the soft sediments (Lundberg et al. 1998).

This geologic history shows that the northeastern part of the South American continent was covered by extended saltwater, brackish water, freshwater lakes, and wetlands over long periods of time. Due to the region's position near the Equator, the climate was hot and humid. Differences between rainy and dry seasons led to water-level fluctuations in rivers and wetlands that in the larger of these took on a monomodal character, because of the large extension of the catchments. These environmental conditions favored the adaptations of plants and animals to periodic drought and flooding and thus to decreased extinction rates.

Paleobotanical evidence for the existence of extended tropical rain forests in South America is exceedingly rare and equivocal for the Cretaceous. In the Paleocene, the only evidence consists of a moderately high pollen diversity. For the Eocene, there are several lines of evidence for the existence of widespread, diverse rain forests taxonomically allied to modern neotropical rain forests (Burnham and Johnson 2004). Molecular-based phylogenies of several lineages of angiosperms, whose modern representatives are now largely restricted to tropical rain forests, indicate a Cenomanian origin (114–98 Ma) (Davis et al. 2002, 2004). They also suggest greater diversity among angiosperms in the Cretaceous, as evidenced by the few fossil records. The large number of fruit-feeding fishes and seed dispersal by fishes (ichthyochory) point to the co-evolution of floodplain forests and fishes. Fossils indicate that over the course of the last 13.5 million years or longer, fish such as tambaqui (*Colossoma macropomum*), which apparently has not changed its diet of fruits and seeds (Lundberg 1998; Lundberg et al. 1998), have persisted. Godoy et al. (1999) provided a preliminary list of 242 riparian tree species common to the Amazon and Orinoco River basin. These authors explained this high number by the past and present connectivity of river corridors.

The development of the extended floodplains along the lower and middle course of the Amazon River and its large tributaries was strongly influenced by a period of climatic changes during the Pleistocene. Several glacial periods led to drops in sea level up to 130 m, increased the declivity of the rivers, and led to deep erosions in the river valleys. This affected the lower courses of the tributaries of the Amazon River in the north and south, until the borders of the archaic shields, and the main stem in the west, up to 2,500 km inside the continent. During interglacial periods, the sea level rose and dammed the rivers back in their valleys. In the following millennia, the rivers filled their valleys with sediments, forming extended floodplains.

This process occurred rapidly in rivers transporting large amounts of sediments from the geologically young, uplifting Andes but slowly in rivers transporting small amounts of sediments from the old archaic shields and nutrient-poor tertiary freshwater sediments from Central Amazonia. Erosion and filling-in of river valleys took place several times, as can be shown by remnants of old river terraces along the Amazon River (paleo-floodplains) (Irion 1984a,b). The Andean zone is geologically very active because the Oceanic Nazca Plate continues to be pushed below the South American Plate. This movement results in uplifting and sinking sub-basins at the eastern pre-Andean zone, generating extended areas subject to periodic waterlogging or flooding (Räsänen 1993).

1.6 Classification of Amazonian Wetland Forests

The zonation of floodplain forests was described in early studies, e.g., by Takeuchi (1962) and Gessner (1968), but Keel and Prance (1979) were the first to provide figures on species distribution with respect to flood depth of an igapó forest of the Negro River, near Manaus. A first approach to classify Amazonian wetland forests according to hydrological and hydrochemical parameters was that of Prance (1979). One of the aims of that study was to define accurately the terminology used for the different types of wetland forests, because in the scientific literature the local terms várzea and igapó were used in different ways. Local people and many scientists applied the term várzea to all types of periodically flooded land (Ducke and Black 1953, 1954), whereas igapó was used to refer to permanently waterlogged swamp forest of the lower Amazon (Richards 1952). Other investigators included forests flooded by blackwater and whitewater under the term igapó (Gessner 1968; Moreira 1970).

Sioli (1956) correlated the hydrochemical conditions in Amazonian rivers with the geology and geomorphology of their catchment areas. Whitewater rivers, such as the Amazon main stem and the Purus, Juruá, and Madeira Rivers, have their origin in the Andes, from where they transport large amounts of nutrient-rich sediments. Their waters have a near-neutral pH and relatively high concentrations of dissolved solids, mainly, alkali-earth metals and carbonates. The electrical conductivity of the Amazon River decreases from about 100 $\mu S\ cm^{-1}$ near the Andes to about 40 $\mu S\ cm^{-1}$ at its lower course, by dilution with water from electrolyte-poor tributaries. Whitewater rivers deposit their sediments in large fringing floodplains, locally called várzea. These are fertile and covered with highly productive terrestrial and aquatic herbaceous plant communities and floodplain forests. Blackwater rivers, such as the Negro River, drain large areas of white sand into the central basin and on the shields. Their water is transparent with low amounts of suspended matter but high amounts of humic acids, which give the water a brownish-reddish color. The pH values are in the range of 4–5 and electrical conductivity is $< 20\ \mu S\ cm^{-1}$. The floodplains of blackwater rivers are of low fertility and locally called igapó. They are covered by a slowly growing floodplain forest in which litter production is 30% lower (summarized in Furch and Junk 1997b) and the diameter-increment rates of trees is up to 50%

Table 1.2 Key to the principle types of Amazonian forests subject to inundation (According to Prance 1979), a-d our modifications

Periodically inundated forest		
Flooded by regular annual cycles of rivers		
Whitewater	1	Seasonal várzea
Blackwater and clearwater	2	Seasonal igapó
Flooded by tidal movements		
Saltwater	3	Mangrove
Freshwater backup	4	Tidal várzea
Flooded by irregular rainfall (flash floods)	5	Floodplain forest[a]
Permanently inundated forest[d]		
Whitewater	6	Permanent swamp forest[b]
Blackwater and clearwater	7	Permanent Igapó[c]

[a] Riparian forests along low order rivers
[b] Várzea swamp forest, várzea chavascal
[c] Igapó swamp forest, igapó chavascal
[d] Long-term inundated forests

lower than in várzea forest species. Terrestrial and aquatic herbaceous plants are scarce and many whitewater species are absent because of the low fertility and/or low pH (Junk and Piedade 1997). Clearwater rivers, such as the Tapajós, Xingu, and Tocantins Rivers, have their catchments in the archaic shields of Guiana and Central Brazil. Their waters are transparent and greenish, with low amounts of sediments and dissolved solids and an acidic pH that in large rivers varies between 5 and 6. Electrical conductivity in the large rivers is in the rage of 20–40 $\mu S\ cm^{-1}$ but in low-order streams can decrease to 5 $\mu S\ cm^{-1}$. The floodplains of clearwater rivers are of intermediate fertility and also called igapó.

Prance's floristic analysis of the different forest types (Prance 1979) supported the view of limnologists and led to the classification shown in Table 1.2.

Puhakka and Kalliola (1993), in their study of wetland forests in the Peruvian Amazon region, used river dynamics as the criterion to differentiate between two major groups: (1) vegetation in the meander zone of rivers, and (2) swamp vegetation in flooded lowlands. The first group is characterized by highly dynamic erosion and sedimentation processes leading to different arrangements of successional stages of herbaceous and forest communities. The second group covers poorly drained, geomorphologically rather stable areas in abandoned floodplains with relatively stable vegetation types that are considered to be in climax (herbaceous swamps, shrub swamps, palm swamps, and forested swamps).

Kubitzki (1989a,b,c) followed the classification of Prance and explained the floristic differences between várzea and igapó as arising from differences in nutrient status. He also pointed to the close floristic ties between floodplain forests and forests in the adjacent uplands (terra firme). Especially close relationships exist between terra firme forests on latosols and várzea forests. Many upland species have developed flood-tolerant ecotypes in the várzea, e.g., *Guazuma ulmifolia* and *Spondias lutea*. The genus *Maquira* (Moraceae) has one species in the várzea (*M. coriacea*), another occurs there facultatively (*M. calophylla*), and others are restricted to the terra firme (Berg 1972). In the western part of the Amazon rain forest, many várzea species also occur on terra firme, e.g., *Ceiba pentandra* and *Pseudobombax munguba*, because of the better nutrient status of terra firme soils near the Andes.

The flora of the igapós has close connections with the woodlands of oligotrophic campinas and caatingas and with those of white-sand savannahs. These areas show periodically high groundwater levels or even shallow flooding and thus require the respective adaptations by trees. Many of these species, such as *Qualea retusa, Panopsis rubescens*, and *Humira balsamifera*, are also found in the upper parts of igapós. In some genera, all species are restricted to periodically flooded habitats, such as *Ramatuella, Haploclathra, Leopoldinia, Glandonia, Pachira,* and *Lophantera* (Kubitzki 1989).

Many species reside in várzea and igapó, among others, *Campsiandra laurifolia, Macrolobium acaciifolium, Symmeria paniculata, Virola elongata, Caryocar microcarpum, Allantoma lineata, Caraipa densifolia, Pachira aquatica, P. insignis, Swarzia polyphylla,* and *Vatairea guianensis* (Ducke 1913; Prance 1979; Kubitzki 1989; Wittmann et al. 2010).

Centers of endemism of floodplain tree species are located in the upper Negro River basin, including the Rio Negro Refuge (Steyermark 1982), the Amazonas Savannahs Refuge (Huber 1982) and parts of the Imeri Refuge of Prance (1973). Endemic to this area are: *Leopoldinia piassaba, L. maior, Mauritia carana, Mauritiella aculeate, Schistostemon oblongifolium*, the genus *Ramatuella, Ocotea esmeraldana, Glandonia williamsii, Asteranthus brasiliensis, Henriquezia nitida, Vitex calothyrsa*, and several species of *Swartzia* and *Macrolobium* (Kubitzki 1989).

We agree with Prance's use of hydrological and hydrochemical parameters to classify wetland forest. However, we consider the term "floodplain forest" of type 5 inadequate, because "floodplain forest" is a general term that can be used for types 1–5, all of which occur on different types of floodplains, in contrast to types 6 and 7, which occur on permanently waterlogged habitats. Forest type 5 flooded by irregular rainfall (flash floods) is a riparian forest along low order rivers and we use this more specific term. All Amazonian flooded forests have to fall dry at least for rejuvenation. Therefore we use the term "long-term inundated forests" instead of "permanently inundated forests". We also consider it inappropriate to denominate várzea swamp forests (type 6) as "permanent swamp forest." Swamp forest is a general category that describes all types of forests on long-term-flooded or waterlogged habitats. Várzea swamp forest and igapó swamp forest correctly describe their respective types according to flooding regime and nutrient status. Locally, these forests are denominated *chavascal*. Ayres (1993) described the chavascal of the Mamirauá Reserve for Sustainable Management, near Tefé, as swampy shrub vegetation with a few higher trees that is nearly impenetrable for humans at low water. It is flooded for 6–8 months per year to a depth of 6–7 m. According to Wittmann et al. (2004), the chavascal is established in poorly drained depressions with waterlogged soils, which leads to an accumulation of organic material. We use this term for this vegetation type as well. To characterize nutrient status, we differentiate between the nutrient-rich várzea chavascal and nutrient-poor igapó chavascal.

1.7 Flood Tolerance and Adaptations for Survival during Periodic Flooding

Flood tolerance is the capacity of higher plants to survive flooding by the development of:

- Anatomical structures, e.g., gas transport systems, which facilitate gaseous diffusion from the shoot to the root
- Morphological structures to cope with periodic flooding (stilt roots, tabular roots)
- Metabolic adaptations to anoxic environments (Crawford 1969)

For most plant species, periodic flooding results in stress. Stress describes external constraints limiting resource acquisition, growth, or the reproduction of an organism (Grime 1989). For plants, the primary constraint imposed by flooding is impeded gas exchange. The diffusive resistance of most gases in water is about 10,000 times greater than in air. There is also a 30-fold drop in oxygen concentration between the gaseous and the dissolved states. In the tropics, oxygen deficiency is pronounced because with increasing temperature the solubility of oxygen in water decreases from about 14.2 mg l^{-1} at 0°C to about 7.0 mg l^{-1} at 35°C. At the same time, microbial oxygen demand increases with increasing temperature and quickly leads, in waterlogged soils, to anoxia, a negative redox-potential, and the mobilization and production of substances potentially detrimental to plant roots, such as dissolved iron and manganese, and H_2S (Piedade et al. 2010).

Oxygen stress in roots is accompanied by a decline in energy levels, a more rapid depletion of carbohydrate reserves, changes in cytoplasmic pH, and ultrastructural alterations. Deep flooding lengthens the diffusion path for gas transport and may reach the photosynthetically active parts of the plant, thereby interrupting CO_2 assimilation and respiratory oxygen supply, and decreasing light availability for photosynthesis.

Plants have developed different structural and metabolic strategies, often linked to the growth cycle and to reproductive strategies, to cope with these conditions (Blom 1990; Voesenek et al. 1992). These strategies include: (1) efficient gas transport, for instance, by surface rooting, diffusion through the gas-space system, formation of aerenchymatic tissue, connective gas flows, and controlled radial oxygen loss to the rhizosphere; (2) metabolic adaptations, such as the control of energy metabolism under oxygen deprivation, the availability of extensive energy resources, the provision of essential gene products, macromolecular synthesis, and protection against post-anoxic injury (Hendry and Brocklebank 1985). Furthermore, there is some evidence linking flooding to hormone-triggered changes in morphology (e.g., the hormones ETH, IAA, GA, CK, and ABA), such as root extension, aerenchyma formation, promotion of shoot extension, stem hypertrophy, and adventitious rooting (Armstrong et al. 1994).

In Amazonia, the first studies on the flooding-tolerance of trees were carried out by Gessner (1968), Scholander and Perez (1968), Joly and Crawford (1982), and Schlüter (1989). Joly (1991) correctly pointed out that in the majority of cases a successful strategy to survive periodic flooding is a combination of morphological, anatomical, and metabolic adaptations. The results of recent studies are discussed in Piedade et al. and Ferreira et al. (2010).

1.8 Determination of Flooding Tolerance in the Field

The efficiency of a given strategy – or a combination of strategies – against flooding or water-logging of the soil defines the flooding tolerance of a species or its ecotypes. Adaptations in the growth cycle and reproductive strategies determine whether a species can establish viable populations in wetlands and which position it occupies along the flooding gradient in a river floodplain. There is no sharp borderline between flood-tolerant and flood-intolerant species, which makes comparative studies, e.g., on tree species diversity in river floodplains, very difficult.

Ecologists consider all tree species that occur in river floodplains as flood-tolerant, because they assume that these trees have survived many flood periods during their life histories. The length of the flood period is an important parameter in quantifying flood tolerance, as shown for some shrubs and trees of the Rhine River floodplain (Table 1.3). However, the total number of flood days may be misleading, when the timing and frequency of the flood events are not given as well. In temperate regions, floods in late autumn, winter, and early spring have little effect on the trees because they are in a physiological resting stage, whereas the effects in late spring, summer, and early autumn are large because at those times the trees are fully active. Furthermore, flood stress for trees growing in a gallery forest of a small river subject to several short flood pulses for 60 days of flooding per year differs from that in a floodplain of a large river subjected to a single flood event of 60 days per year.

Table 1.3 Flooding tolerance of tree species of the Rhine River floodplain. Data are given for trees on the lowest-lying habitats during a 10 year period (Dister 1983)

	Length of inundation (days)[a]		
Species	Minimum	Maximum	Depth (m)
Salix alba	190	300	4.80
Ulmus minor, U. laevis	100		
Quercus robur	97	217	4.25
Crataegus monogyna	40	120	
Fraxinus excelsior	40	102	
Acer pseudoplatanus	8	35	
Corylus avellana	3.5	22	

[a] 20–50% of the inundation days fall in the period of low physiological activity

In their natural habitat, trees are distributed along a flooding gradient in a characteristic pattern that is determined by abiotic and biotic factors. Abiotic factors are length, depth, frequency, timing and shape of the flood pulse, current velocity, sedimentation rate, sediment quality, erosion, drought stress at the low-water period, and, in temperate regions, ice damage. Biotic factors are competition, organic-matter content and related oxygen concentrations in soils, seed dispersal, and seedling establishment. Large trees survive floods better than small trees, because flood length is often correlated with flood depth, and many trees cannot tolerate total flooding during the growth period. Trees distributed in the lower ranges of the flooding gradient rejuvenate only in years of very low flood levels (Oliveira Wittmann et al. 2010). However, the growth form of the species can also influence its position on the flooding gradient. In the Rhine River floodplain, the shrubby *Salix purpurea* grows on a higher position than the tree *Salix alba*, not because of lower flood tolerance but to avoid total flooding (Dister 1983). Some floodplain species, such as *Salix* spp. and *Populus* spp. in temperate regions, and *Salix humboldtiana*, *Alchornea castaneifolia*, and *Pseudobombax munguba* in the Amazon várzea, require vegetation-free sediments for germination and seedling establishment. Little-disturbed habitats that are quickly occupied by fast-growing herbaceous plants hinder seedling establishment by these tree species due to shading, despite a tolerable flood stress.

In the humid tropics soil saturation with water and following short anoxic conditions because of high microbial activity under high temperature may occur frequently after heavy rains in many habitats that are not considered wetlands. These conditions may favor a predisposition for flood tolerance in many tropical rain forest species, as shown by Lopez and Kursar (1999, 2003). Frequent short floods in gallery forests along small streams and in depressions select for flood tolerance. The flooding of large, rain-water-fed interfluvial floodplains can last many months but is shallower than that of large-river floodplains, such as the várzeas and igapós of the middle Amazon and its tributaries, where flooding in the low-lying parts is long-lasting and up to 15 m deep. This sequence is reflected by the difference between high-várzea and-low várzea forests and their relationships to the non-flooded upland forest (Wittmann et al. 2010).

The distribution of plant communities along the flooding gradient of the middle Amazon River and information regarding the length of the flood period was provided by Junk (1989). As seen in Figure 1.4, the lowest part of the flooding gradient is covered by short-lived annual grasses, sedges, and herbaceous plants that build a flood-resistant seed bank in the sediment. Higher up on the gradient, perennial aquatic grasses are established that have their growth period during high water and re-establish their populations vegetatively or by seeds during low water (*Echinochloa polystachya, Paspalum repens*). Other species have their growth period during the low-water season, survive flooding with flood-resistant stems, and vegetatively re-establish their populations during the low-water season (*Paspalum fasciculatum*). These vigorously growing grasses occupy a position on the flooding gradient that can also be occupied by trees. They suppress, often for many years, sapling establishment by intense competition for light. Flood-resistant shrubs

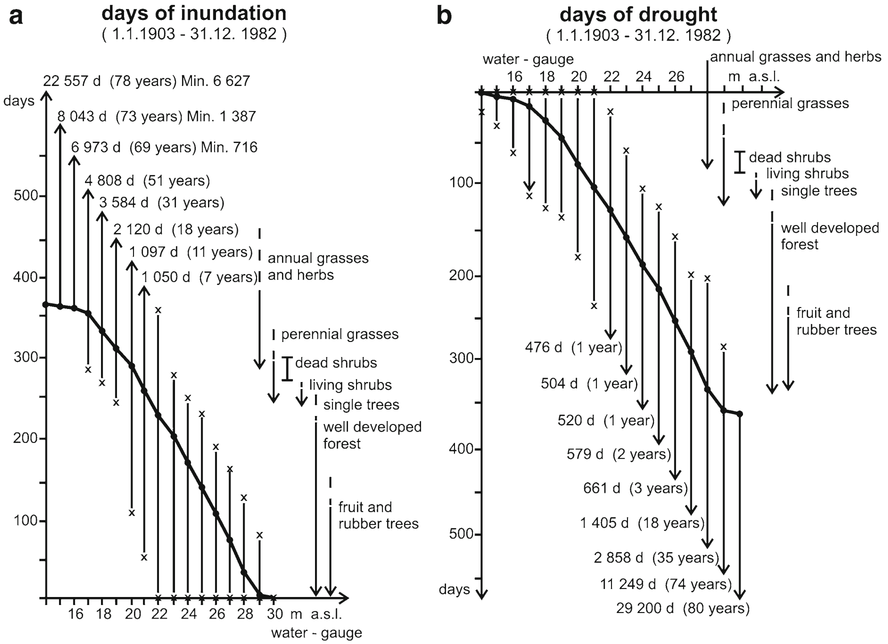

Fig. 1.4 Distribution of major terrestrial plant communities on the flood-level gradient of the Amazon River floodplain near Manaus. The data are based on the 80-year average maximum and minimum numbers of consecutive dry and flood days (hydrological data from Manaus harbor). Totals of the number of years without dry and flood periods are indicated in parentheses. Values are calculated according to the hydrological year (Junk 1989)

(*Cocoloba ovata, Symmeria paniculata, Eugenia inundata*) grow on habitats that are inundated during nearly 9 months per year on average, but can tolerate extreme periods of 3 years of consecutive flooding of the rhizosphere. A species-rich floodplain forest establishes on areas flooded on average during 8 months of the year or less, but single specimens on low-lying areas can also tolerate flooding during two consecutive years. Near Manaus, Igapó forests colonize areas about 1 m lower on the flooding gradient, probably because water is not anoxic near the bottom. The flood tolerance of certain fruit trees, such as mango, bread fruit, and coconut, is economically important. Based on the high species diversity of Amazonian floodplain forests, we postulate that the diversity and complexity of strategies that have evolved to deal with flooding are much higher than in floodplain forests of temperate regions (Wittmann et al. 2010).

To what extent periodic flooding is a pre-requisite for the growth of floodplain trees is an open question. In most tree species, wood increment increases with increasing length of the terrestrial phase. Our preliminary experiments, in which floodplain trees were planted in non-flooded areas, showed positive results when saplings, during the first years, received additional fertilization and were protected against competition from other species and from the attack of herbivorous insects. This observation points to a competitive disadvantage of these species against terra firme species. Growth of *Vochysia divergens*, a flood-tolerant tree species from the Pantanal of Mato Grosso, is correlated with rainfall, implying that water shortage may be a limiting factor. These assumptions have been corroborated by the observation that many species of the high várzea forest in western Amazonia also occur on non-flooded habitats with better nutrient supply and high rainfall (Kubitzki 1989).

The seed-dispersal strategies of many species illustrate the importance of water for the maintenance of viable populations. Many species, such as *Panopsis rubescens, Swartzia polyphylla, Cynometra spruceana, Glandonia* spp*.,* and *Burdachia prismatocarpa*, have developed floating fruits or seeds to facilitate dispersal by water (Kubitzki 1989, Parolin et al. 2010b). Others species of seeds are distributed by fishes, e.g., *Bactris* sp*., Calyptranthes ruizana, Pseudoxandra* sp*., Genipa americana, Byrsonima* sp*., Mouriri* sp*., Endlicheria* sp*., Tetragastris unifoliata,* and *Quiina rhythiodopus* (Goulding 1980).

1.9 The Use of Amazonian Floodplain Forests

With up to 28 (mean 14.6) persons per square kilometer, Amazonian whitewater river floodplains were densely colonized already in pre-Columbian times (Denevan 1976). However, we may assume that the impact on the várzea forest was relatively small, because there was little demand for wood and arable land, and there was no need to increase pasture area because large-scale animal ranching was not known. Forest destruction started in the middle of the nineteenth century with the enormous demand for wood to fuel the engines of steamships. Agriculture and cattle ranching started on a small scale around Belem and Manaus, but at the beginning of the twentieth century spread from Belem up-river. In 1929, jute cultivation for fiber production began near the city of Parintins and reached 25,000 t in 1953. By the time the boom had started to decline in the 1970s, because of competition from plastic sacks and cheap fiber from Bangladesh, large areas of the lower Amazon River floodplain had already been deforested (Gentil 1988; Goulding et al. 1996).

Selective logging decreased the stocks of a few preferred timber species of medium to high wood density that were later substituted by others (Schöngart, Schöngart et al. 2010a). These were exploited in the same unsustainable manner, i.e., first the forests near urban centers and later also those in remote areas were degraded. For the last several decades, softwood species, such as *Ceiba pentandra*, have been heavily exploited for plywood production. Previously very common in the várzea, this species is now rare with very little regrowth. Selective logging reached the Amazon tributaries in the 1980s, after most floodplain forests along the main river had been selectively logged. Today, most wood used in cities along the Amazon River still comes from the floodplains of the upper Solimões, Madeira, and Purus Rivers, but commercially exploitable forest resources are nearly depleted. During the entire period of forest exploitation, there has been very little regrowth because, with increasing agriculture and cattle ranching, high várzeas were deforested. These areas provided fertile soils for sufficiently long dry periods of crop and pasture plantations. Today, most floodplain forests on the lower Amazon River are species-poor secondary forests, and the few remnant mature forests are heavily degraded. Nearly pristine forests still remain in Brazil at the middle Solimões, mainly in the Sustainable Management Reserve of Mamirauá, near the city of Tefé.

Today, the heavy pressure exerted by farmers, cattle ranchers, and logging companies on the forests continues, and management concepts are urgently required to avoid the destruction of this unique forest type. The várzea is one of the very few sites in central Amazonia where the nutrient stock in the alluvial soils is replenished by the annual floods and is sufficiently high to allow the sustainable production of timber and non-timber products (Furch 1997, 2000). Several native floodplain tree species show fast growth rates and are of interest for the timber market. They provide economically viable and ecologically sound options for the local inhabitants as well as the timber industry (Wittmann and Oliveira Wittmann 2010). Other services of the floodplain forests, such as river-current breakers, protection of the floodplain against erosion, carbon sink, habitat and food source of many animals including economically important fish species, gene pool of flood-tolerant species or ecotypes, etc., are of major importance for humans and the ecosystem, but are little acknowledged by planners.

Technical assistance for várzea forest management cannot be expected from forestry in the Amazonian terra firme, which to a large extent is restricted to non-sustainable timber extraction, frequently followed by transformation of the plots to pasture or soybean plantations. Only a few enterprises are attempting to manage upland forests sustainably. However, the management methods of these forests cannot be applied to várzea forests, because the environmental conditions in floodplains are quite different. Instead, specific management systems for floodplain forests are required (Schöngart 2010). A fundamental deficiency of management concepts in most tropical rain forests is the lack of precise information about the growth rates of individual trees in the stands. The small differences in rainfall between the dry and rainy seasons lead to the barely pronounced formation of annual rings in many Central Amazonian terra firme tree species, which makes the determination of aging by tree-ring analysis difficult. In várzea and igapó, the heavy stress of prolonged deep flooding leads to a reduction of diameter increment and the formation of well-developed growth rings in many tree species, even in those that do not shed their leaves and that are photosynthetically active during the flood period. The development of a methodology to determine individual growth rates and wood production by tree-ring analysis is a pre-requisite for the establishment of growth models of different tree species and the basis of management concepts (Worbes 1984, 1989; Worbes and Junk 1989). It will allow the sustainable use of floodplain forests by protecting their species diversity along with the other benefits of these ecosystems (Worbes and Fichtler 2010).

1.10 Discussion and Conclusions

Inventories indicate that Amazonian floodplain forests are the most diverse wetland forests worldwide, containing more than 1,000 tree species (Wittmann et al. 2006a). Geological evidence supports the existence of extended wetlands since the Early Cretaceous period, when South America separated from Africa. Furthermore, the position of the Amazon River basin near the Equator provided relatively high paleoclimatic stability. These conditions favored the development of adaptations by trees to periodic flooding and diminished the risk of species extinction during adverse periods.

Different types of wetlands cover large areas of tropical and sub-tropical South America. In all of them, flood-tolerant trees play an important role in the vegetation cover. Individual trees and forest patches occur in flooded savannas, while strips of riparian forests accompany savannah and forest streams, and mangroves grow on the coastline. About one million square kilometers, corresponding to 14% of the Amazon basin, are covered by wetland forests. A major portion of these forests is located in narrow strips along low-order streams and rivers. Extended swamp forests are found in interfluvial areas in the Amazonian lowlands. Of great economic importance are the floodplain forests along the Amazon River and its large whitewater, clearwater, and blackwater tributaries, the várzea, and igapó. These cover an area of about 400,000 km^2 (Junk 1997b). Várzea forests are under particularly heavy human pressure, since most of the timber used in urban centers along the Amazon River is logged in these forests. Fertile alluvial soils in the várzea attract farmers and cattle-ranchers, who destroy the forest for crop and pasture plantations. Today, floodplain forests along the lower Amazon River are heavily degraded, and selective logging has modified species composition along most of the river's tributaries. In Brazil, major areas of nearly pristine várzea forests still exist in the Reserve for Sustainable Management of Mamirauá, at the confluence of the Japurá and Solimões Rivers.

Despite the economic and ecological significance of Amazonian large-river floodplain forests, ecological knowledge is limited. Until the 1970s, studies in the Amazonian floodplain forests were mostly carried out by botanists, who provided the taxonomic basis for further research (Ducke and Black 1953, 1954; Takeuchi 1962; Pires 1961; and others). In the following years, several studies greatly improved our understanding of floodplain forests. Prance (1979) classified wetland forest types according to hydrological, chemical, and floristic parameters. His classification was in agreement with that of limnologists (Sioli 1956; Irmler 1977) and ended terminological confusion in the scientific literature. Floristic studies in the pre-Andean zone called attention to the importance of river dynamics in the development and maintenance of Amazonian biodiversity (Salo et al. 1986). Junk (1989) was the first to quantify flood stress by correlating the length and depth of flooding with the occurrence of plant species and communities in the várzea. Kubitzki (1989) showed the floristic relationship of várzea forests to nutrient-rich terra firme forests on latosols in eastern Amazonia and of igapó forests to oligotrophic terra firme woodlands of campinas, caatingas, and white-sand savannahs.

Of fundamental importance for productivity studies was the description of annual growth rings in floodplain tree species (Worbes 1984; Worbes and Junk 1989). It allowed calculation of the wood increment of individual trees and established the basis for the first sustainable management concept of tropical rain forests, based on individual growth rates over the entire life span of the trees. These studies presented the basis for a period of intensive research in the Central Amazon River floodplain by a team of Brazilian and German scientists in the frame of a cooperation treaty between CNPq, on the Brazilian side, and the Max-Planck-Society and BMBF (during 12 years) on the German side. The work was carried out by investigators at the INPA (Manaus) and MPIL (Plön).

The results of these studies and the remote sensing data obtained by a team of scientists at the University of Santa Barbara, California, are presented in this book and provide a synopsis of the current state of knowledge concerning the ecophysiology, primary production, biodiversity, and sustainable management of Central Amazonian floodplain forests.

Chapter 2
Development of the Amazon Valley During the Middle to Late Quaternary: Sedimentological and Climatological Observations

Georg Irion, José A.S.N. de Mello, Jáder Morais, Maria T.F. Piedade, Wolfgang J. Junk, and Linda Garming

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Abstract Pleistocene sea-level changes affected the Amazon River as far as 2,500 km inland. This results on one hand with the formation of large floodplains of the Amazon and the lower parts of its tributaries during sea-level heights and on the other hand with a deeply incised river system during low sea-level stages. This was most effective since Mid-Pleistocene when the changes of sea-level got stronger. This could be shown from the deeply incised valleys of Negro and Tapajós Rivers. During Last Glacial Maximum the slope of the Amazon below its junction with Tapajós River increased by the factor 10, resulting probably in a braided River. Paleofactors of sediment cores taken from Central Amazonia lakes and from Tapajós River give no hint for a significant change in climate.

2.1 Introduction

While, in general, the effects of Quaternary sea-level changes are restricted to coastal areas, in estuaries they may be observed as far as several hundred kilometers inland. In the case of the Amazon River, the impact of such inland changes extends over more than half of the continent, some 2,500 km upstream from the mouth of the Amazon. This results in far-reaching sedimentary changes, especially in the main valley of the Amazon River and in the lower sections of its tributaries. Accordingly, the sedimentological development of the Amazon valley has long been the focus of great interest. When were the deeply incised valleys of the Amazon lowlands formed? What residues, mainly of the Pleistocene warm periods, can be found? What significance and ecological impact do these relicts have on the present appearance of the river floodplains? These questions, together with the important role played by lake deposits as paleo-indicators in respect to in climate and ecology will be discussed in this chapter.

2.2 Formation of Ria Lakes

Ria lakes are relicts of former, deeply incised river systems (Gourou 1950) and are filled with (fresh) water. In the Amazon basin, thousands of such lakes occupy the lower sections of rivers and creeks. In the case of the Negro, Xingú, and Tapajós Rivers, Ria lakes achieve lengths of more than 100 km, although there are also thousands of lakes whose lengths barely exceed 1 km. Ria lakes only occur in the valleys of rivers with a low sediment load. Rivers with a high sediment load, such as the Madeira, Purús, and Juruá Rivers, do not show this phenomenon as the corresponding valleys became filled with river sediments long ago.

All Ria lakes show a high degree of padding. In many of these lakes, the bottom is exposed during low water levels and creeks may form for several months, acting as a local drainage system. It is assumed that an equilibrium develops between sedimentation and erosion during high- and low-water stages. As a result, water depth in Ria lakes scarcely exceed 5 m during average water stages. This was observed in

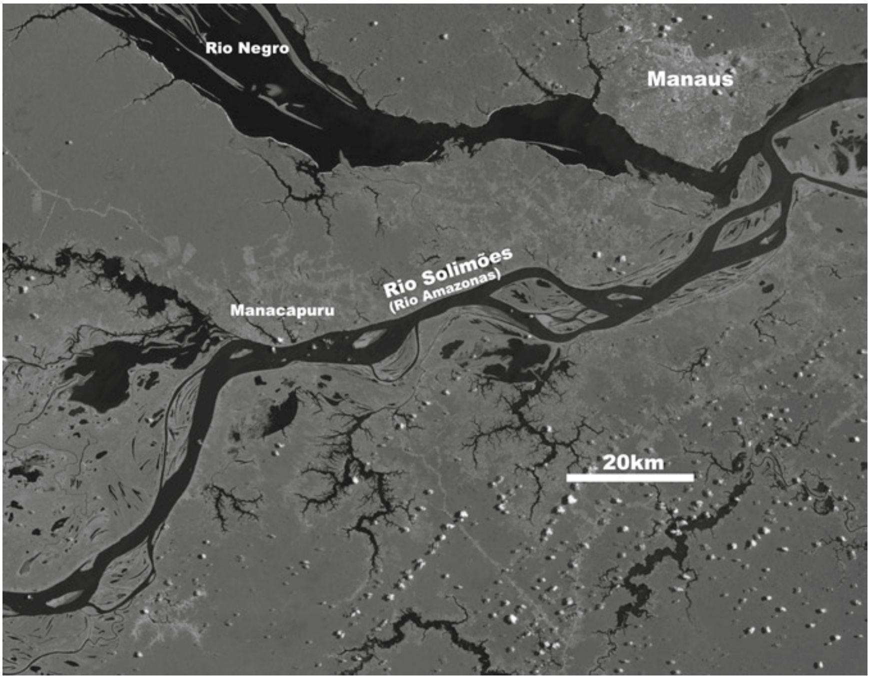

Fig. 2.1 Satellite image of the Solimões River and its surroundings, between Manacapuru and Manaus. Note the large numbers of smaller Ria lakes south of Rio Solimões. The lower section of the Negro River, as shown in the upper part of the figure, is itself a Ria lake

the intensively studied areas north and south of the Solimões River (Fig. 2.1), between Manacapuru and the Solimoes/Negro junction, and, e.g., for the Ria lakes of the Uatuma and Juruti Rivers (own field studies in 1992).

The large extension and comparatively low sediment load of the Negro and Tapajós Rivers results in higher water depths in the corresponding Ria lakes (respectively, 100 and 50 m), with one exception: the Trombetas River. The valley of this river is filled and a new riverbed has formed on top of the deposited lake sediments. However, in its tributaries, Ria lakes are still present.

It has been suggested that Ria lakes resulted from the filling of troughs that formed during low sea-level stages, when large parts of the Amazonian River system were deeply incised. While this explanation is generally accepted, the time component is still debated. It may be assumed that trough formation started with the initial lowering of the Pleistocene sea-level, or that it resulted, at least in part, from tectonic movements (Latrubesse and Franzinelli 2002), but unambiguous geological evidence is lacking. Many Ria lakes were formed during the Last Glacial Maximum (LGM), as is discussed later in this chapter. Other such lakes, mainly those surrounded by Tertiary geological formations, may be older. A closer study of the lower sections of the Negro and Tapajós Rivers, the largest Ria lakes of Amazonia, revealed important information regarding the evolution of the river valleys, which reaches back far beyond the LGM.

2.3 Mid to Late Quaternary Changes in the Lower Rio Negro Valley

Some 140 km downstream of the Negro and Branco River junction, the Negro River leaves an area of Devonian shale and enters one of Cretaceous sandstone, which is relatively vulnerable to erosion. Further downstream, there is a deeply incised riverbed that reaches a maximum depth of 100 m and is not completely filled with sediments (Fig. 2.2). Presumably, the valley was formed during the Pleistocene low-water stage, during which the low sea-level, 120–130 m below pMSL (present mean sea-level), was similar to that reached during the LGM. This resulted in a lowering of the water level of the Negro River by at least 40 m at its mouth (see below).

The results of 3.5-kHz profiling in the Negro River valley have shown that, in the Holocene, a 10-m-thick sediment layer was deposited in large parts of the valley during high sea-level stages (Irion et al. 1999). The volume of this Holocene deposit is estimated to be one third of the total sediment mass deposited during the existence of the deeply incised trough of the Negro River valley. Since similar processes occurred during each sea-level height of the Late Quaternary, the trough filling is comparatively young, i.e., not older than a few glacial cycles. This fits very well with

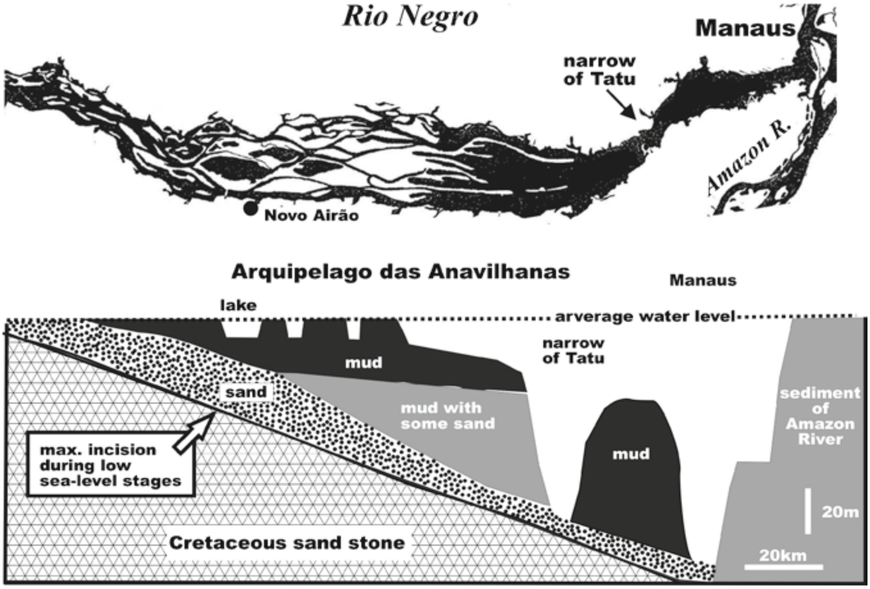

Fig. 2.2 Cross-section through the Ria lake of the Negro River. The archipelago of the Anavilhanas formed during various sea-level heights during the last about 800,000 years. The sediments are predominantly fine-grained and were deposited as a result of decreased flow in the upper 100 km of the river. At the narrow of Tatu, where the width of the river decreases to merely 1.6 km, the deposition of mud is interrupted, but it continues when the Ria lake expands again directly upstream of Manaus. Maximum incisions of the Negro River are reached during low stands of the sea-level

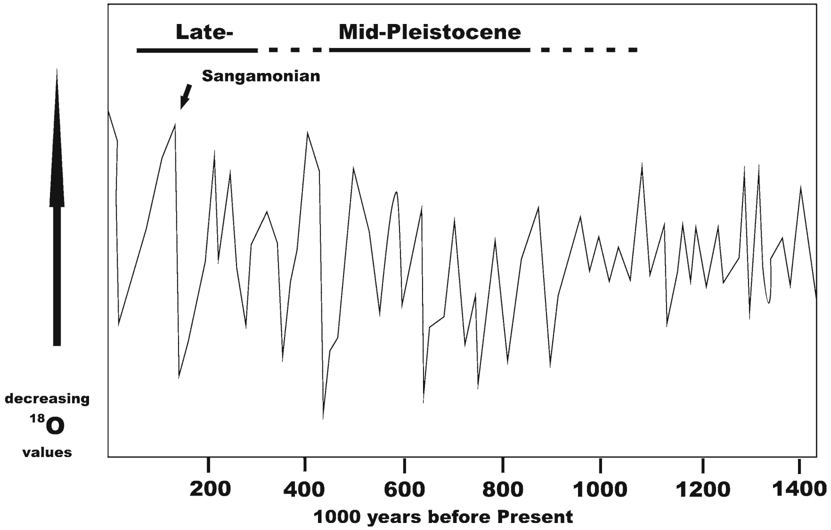

Fig. 2.3 Oxygen isotope curve of the foraminifer *G. sacculifer* as determined in a deep-sea core (ODP leg. 130 core 806 – redrawn from Berger and Wefer 1992). The difference in ^{18}O values is small but significant. Low ^{18}O values correspond to high sea-levels (recent time, Sangamonian, etc.) and high values to sea-level minima. Note the strong increase in the oscillation between high and low ^{18}O values at about 800,000 years BP. Deeply incised Ria valleys, such as those of the Negro and Tapajós Rivers, may have formed during these times as a result of fluctuating sea-levels

the general trend of sea-level fluctuations during the Quaternary, as determined from the δ^{18}O variations in deep-sea sediment cores. There is evidence that a change to more extended glaciations occurred approximately 600,000–900,000 years ago, the so-called Mid-Pleistocene revolution (Berger and Wefer 1992; Fig. 2.3).

It has been estimated that, during the Early Pleistocene, the drops in sea-level were significantly smaller than those that occurred during the LGM, i.e., in the range of 40 m. According to our analyses, performed on sediment cores recovered from Central Amazon lakes and from the Tapajós River (see below), a sea-level of 40 m below the pMSL would have lowered the mean river level at Manaus by a maximum of 13 m. This is only a few meters below the average yearly minimum level of the Amazon at this site. In contrast, during the LGM, the mean river level at Manaus was more than 40 m lower.

During the Mid-Pleistocene Revolution, the Negro River incised and formed its valley, destroying all relicts of a smaller pre-existing "Ria valley." The surrounding Cretaceous sandstone was easily eroded, weakened by weathering processes during the Tertiary. During the Mid-Pleistocene and Late Pleistocene, the high sea-level resulted in the deposition of fine-grained river sediments in the newly formed trough. Like those deposited during the Holocene, these sediments were soft and would have been immediately eroded by flowing water. However, during low sea-levels they were exposed to the atmosphere and consequently oxidized to a depth of several meters. All organic carbon was reduced, accompanied by the alteration and neo-formation of minerals, mainly lepidocrocite, Al-chlorite, anatas (TiO_2), and iron oxides (Keim et al. 1999). These processes led to extensive hardening of the sediment surfaces such that they became resistant to erosion. Similar hardened surfaces are found in many lakes below the Holocene mud, e.g., in those of the Negro and Tapajós Rivers and in smaller lakes in Central Amazonia (e.g., Lago Calado, Keim et al. 1999). Presently, the 140-km-long Ria lake of the Negro River valley is nearly completely filled with sediments between Airão and the narrow at Ilha Tatu. Additionally, sediments have been deposited in the enlargement north of Manaus.

2.4 Mid to Late Quaternary of the Lower Tapajós River Valley

The Ria of the Tapajós River is 150 km long and 20 km wide. During high-water stands, the backwater effect reaches as far as Itaituba, which lies about 225 km from the mouth of the Tapajós River. In contrast to the Negro River, there are no islands in the Tapajós River, but the upper half of the valley has filled to the extent that, during low-water periods, sediments covering an area of several hectares fall dry.

Since the high gas content of the sediment prevented 3.5-kHz profiling, the limits of the Holocene sediment masses were detected by about 50 profilings, reaching down to pre-Holocene sands or to the above-mentioned oxidized lake deposits. Figure 2.4 shows that the filling process is by no means complete. As a result, it seems that the original Tapajós valley did not form before the above-mentioned change in glaciation intensity.

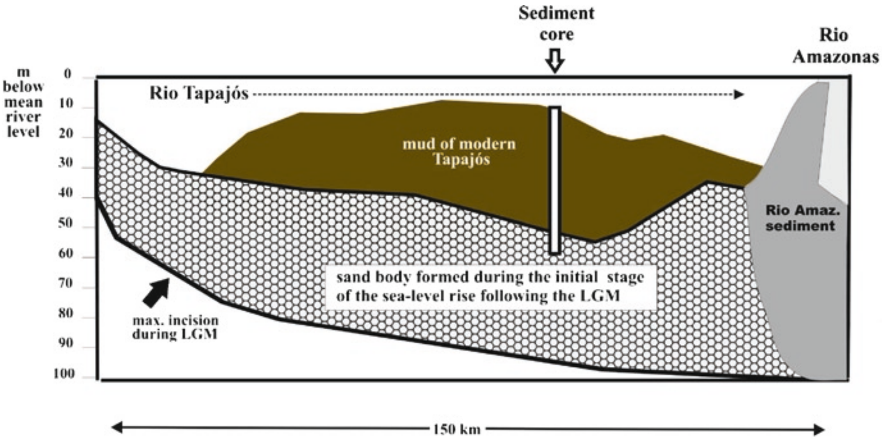

Fig. 2.4 Cross-section through the Ria lake of the Tapajós River as detected by profiling during field trips in 1999, 2002, and 2005. The profile follows the deepest incision of the Tapajós River bed, during the LGM; later, the river bed filled with fine-grained sediments. Older sediments extending on both sides of the deepest incision and reaching close to the surface – not shown in the graph – occupying more space than Holocene sediments

2.5 Formation and Distribution of the Palaeo-Várzea

Today's várzeas were formed during the Holocene, when large parts of the Amazon valley were submerged due to the backwater effect of the high sea-level. Consequently, in the Pleistocene, there must have been extended floodplains during each change in sea-level that was higher or similar to its precursors. The most extended várzea was formed during the last warm period, the Sangamonian. The extent of this palaeo-várzea can be estimated from radar maps of the Projeto Radam, published in 1970–1972. The total area remains difficult to estimate but must have been far greater than 50,000 km². The largest areas are located in the vicinity of Lago Amanã, some 70 km north of Tefé, between Lago Coari and the Purús River, south of the lower Rio Solimões, as well as at the rim of the várzea between Juruti, Óbidos, and Santarém. Palaeo-várzea can be recognized by the sequences of ridges and swales that resulted from rhythmic depositional processes occurring predominantly at the slip-off slope of the river course (Irion 1976a). The structure of the paleo-várzea is the same as the recent várzea, but its features have been significantly weakened. Additionally, in many areas of the paleo-várzea, Ria lakes are present. Those várzeas most probably have formed earlier than the LGM, during a sea-level higher than the present one.

Sediment cores taken from the paleo-várzea show significant alteration in mineral composition due to weathering processes at and near the surface; however, with increasing depth (several meters), the mineral composition is the same as that of nearby recent river deposits. The alterations consist of increased amounts of kaolinite, gibbsite, and iron oxides at and near the surfaces of the paleo-várzea (Irion 1984a), sometimes accompanied by a decrease in smectite. The well-preserved surfaces and the presence of only moderate alteration in the minerals of the surface sediments are in accordance with the Sangamonian age of the paleo-várzea. There are also relicts of older Pleistocene stages; these show a higher degree of alteration than those of the Sangamonian várzea (Irion 1984a).

Most of the smaller Ria lakes are situated in the várzeas that formed during the last sea-level high, the Sangamonian, and are approximately 110,000 years old (see below). The troughs of those lakes may have formed during the LGM but precursors of Mid-Pleistocene to Late Pleistocene age may have been present at the same place. For example, there are numerous smaller lakes in the paleo-várzea south of the Solimões River, between the city of Manacapuru and the Solimões/Negro junction; or in the triangle west of the lower Purus and Solimões Rivers. Here, two generations of paleo-várzeas may be clearly distinguished by their different altitudes, as shown by the georeferenced altitude program of NASA (Fig. 2.5). Sediments profiles taken from the paleo-várzea of the region surrounding Lago Aiapuá show, due to the well-preserved mineral association, that this várzea cannot be older than of Sangamonian age (Irion 1984a).

The NASA georeferenced altitude program shows that the paleo-várzeas are between 15 and 20 m higher than the recent várzea. The recent river level at Manaus is 20 m above pMSL and reaches 45 m above pMSL at Tefé. The surfaces of the paleo-várzeas rise from Manaus to Tefé, from 40 to 60 m above pMSL.

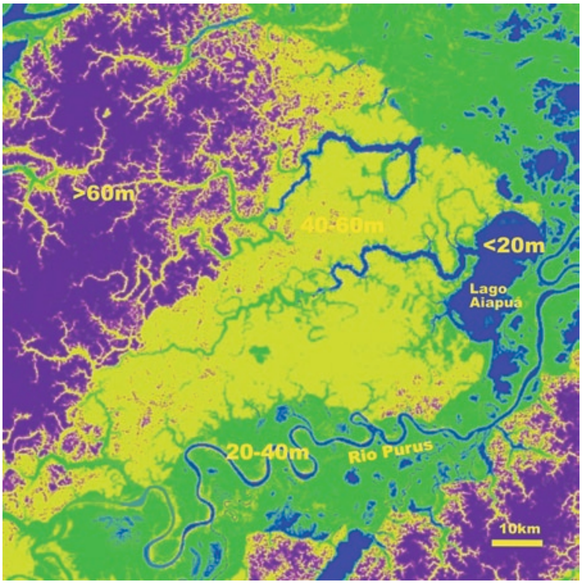

Fig. 2.5 Altitude map of the area west of the Purus River and showing Lago Aiapuá (NASA georeferenced map). Three different generations of várzea can be identified. In the south and west recent várzea 20–40 m above msl, lower paleo-várzea, most probably of Sangamonian age, 40–60 m above msl, and an older várzea >60 m above msl. The large relative differences in heights can be explained by slow, tectonically upward movement

These high positions of the paleo-várzeas can not only be explained by higher sea-levels in the Sangamonian and during older, warm Pleistocene periods; additionally, there should be a decreasing difference between recent várzea and paleo-várzea surfaces with increasing distance from the sea. Regarding paleo-várzea older than 110,000 years, slow tectonic upward movements at least partly explain this phenomenon. These results are in accordance with those of Dunne et al. (1998), who provided evidence for an upward tectonic movement in the western Amazon basin at Purus and Jutai Arch. An uplift in the eastern Amazon basin is less probable and explains why, in the region downwards of Óbidos, there is no significant height difference between recent and palaeo-várzeas.

Despite a serious lack of detailed studies of the paleo-várzea, we drew maps of their distribution using NASA radar maps and the results of the Projeto Radam. The three maps shown in Figs. 2.6–2.8 may be regarded as a preliminary approach to the distribution of the Amazonian paleo-várzeas.

As is the case for many other tropical lowland areas, the Amazon basin is characterized by extremely low fertility (Weischet 1977). However, in contrast to the large area of the Precambrian shields and the Cretaceous/Palaeozoic formation, the várzea is highly fertile (Sioli 1957). The Na, Ca, Mg, and K distributions in the fine fraction of the soils serve as representative benchmarks. Figure 2.9 shows the large differences between the old surfaces and the várzea, but there are also differences between Pleistocene and recent várzeas.

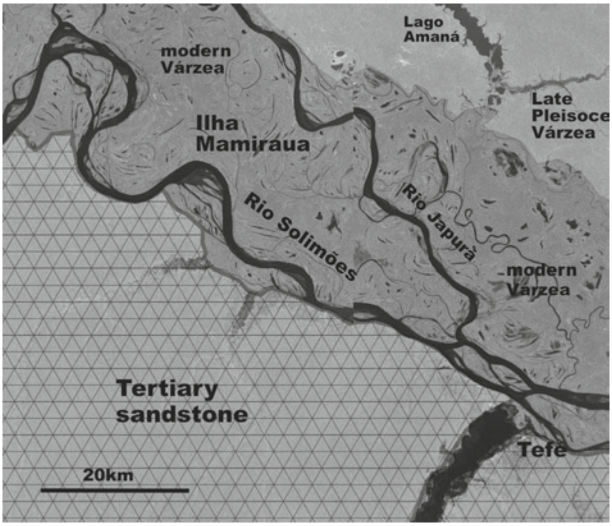

Fig 2.6 Radar map of the Lago Amanã area showing the palaeo-várzea and the recent várzea of Ilha Mamirauá, near Tefé. There are no detailed descriptions of the sediment profiles that would have allowed estimation of the age of the várzea; but from observations made during a field trip in 2002 (Inpa/MPI-Plön/Senckenberg-Inst.) it can be concluded that there are at least two generations of palaeo-várzea along the banks of Lago Amanã

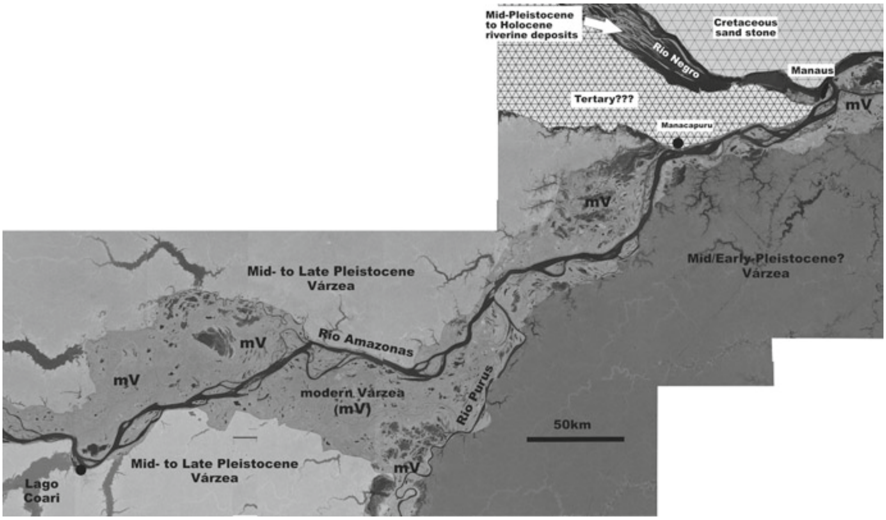

Fig. 2.7 The Amazon valley between Lago Coari and Manaus. Note the extremely large area occupied by Mid-Pleistocene and Late Pleistocene várzeas. Várzeas of three different ages are distinguished not only by differences in their heights but also by differences in the degree of alteration of their mineral compounds (Irion 1984a). The modern Amazon valley (50 km) is considerably wider between Coari and Manacapuru but subsequently narrows to less than 10 km

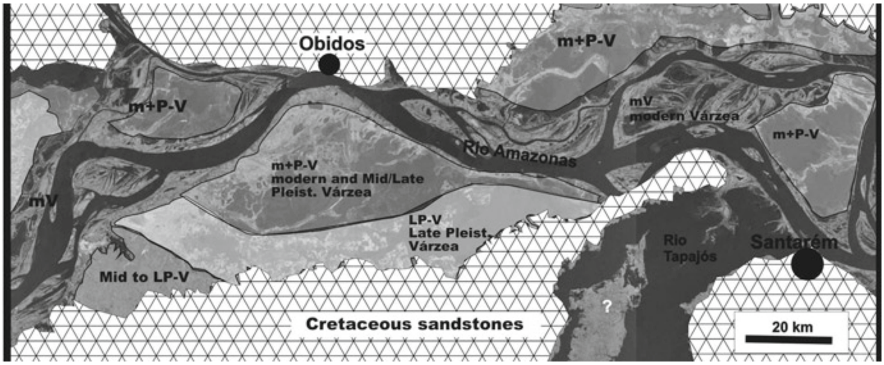

Fig. 2.8 The broad extent of the várzea of the Santarém/Óbidos area. Field studies done in 2005 (Irion unpublished) showed that modern várzea and Late Pleistocene várzea occur on similar levels. During flooding in June, July, and August, these areas are drowned. Sioli (1957) pointed out that this section of the Amazon River floodplain has not yet filled with sediments

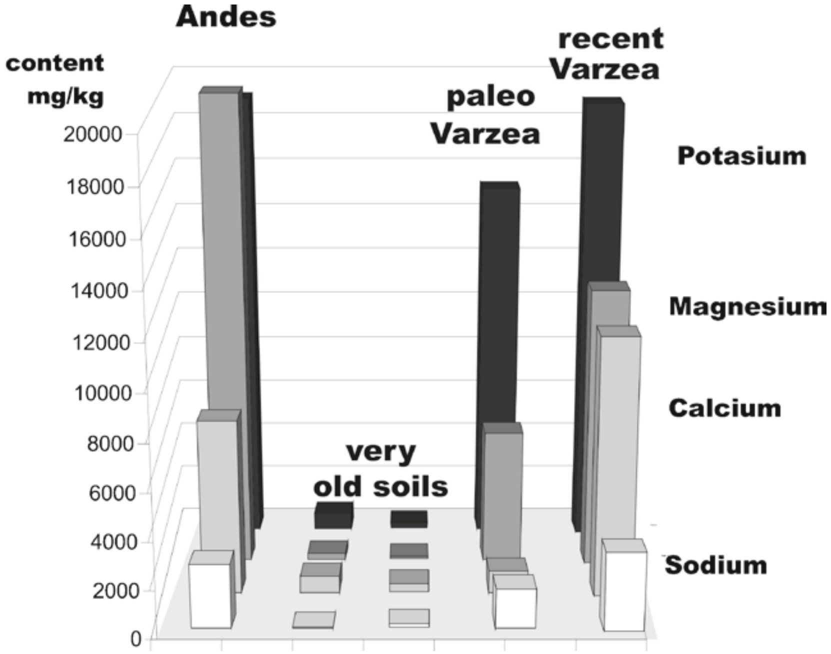

Fig. 2.9 Potassium, calcium, magnesium, and sodium in Amazonian soils in grain-size fraction <2 µm (After Irion 1976b). Note the large differences between the old surfaces and the várzeas and the Andes. The differences in the contents are between one and two orders of magnitude. The fertility of the somewhat richer soils of the Paleo-Várzea is higher, as shown, for example, by the higher density of rubber and paranut trees than of the Belterra clays (indicated as very old soils)

2.6 The Paleo-Climate During the Late Holocene: An Analysis of Palaeo-Proxies from a 50-m Core Recovered from the Sediments of Lago Tapajós

Climate development in the Amazonian lowland has been discussed vehemently over the last several decades (Haffer 1969; Prance 1982, Colinvaux et al. 2001), underlining the need for appropriate paleo-indicators. In this context, sediments and thus sediment cores of Ria lakes are an appropriate paleo-indicator. The following discussion is based on our studies of Ria lakes in central Amazonia (Keim et al. 1999; Behling et al. 2001) and in the Tapajós River (Irion et al. 2006). It focuses on the results obtained from a sediment core recovered from "Lake Tapajós" (Irion et al. 2006).

A 50-m sediment core (see Fig. 2.10 below) was removed from the Ria lake of the Tapajós River, at a location of about 2° 47′S and 55° 05.5′W′, 60 km south of the river mouth at Santarém (Irion et al. 2006). The initial expectation was to recover lake sediments deposited 14,000 years ago. However, this turned out to be

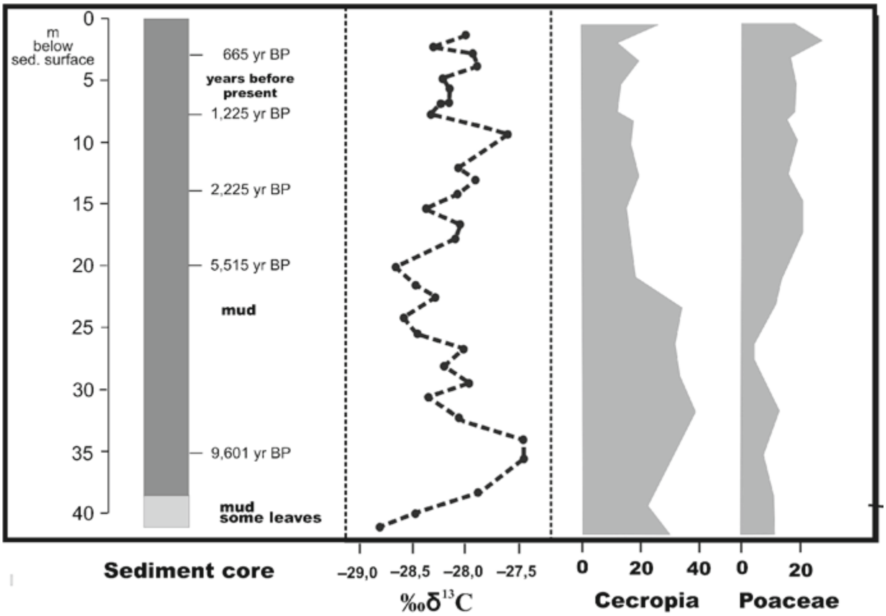

Fig. 2.10 δ^{13}C, and Cecropia and Poaceae pollen records in the long sediment core taken from the Tapajós Ria Lake, located at 02° 47'S/55° 05.5'W (Irion et al. 2006). δ^{13}C measurements showed that no or only small amounts of organic compounds are representative of C_4 plants, indicating that forest has always been the dominant vegetation in the drainage area of the Tapajós. The consistent vegetation cover is also evidenced by the mineralogy and the pollen distribution (see text)

impossible because a huge sand body had been pushed onto the older sediments during the Late Pleistocene rise of the lake level (caused by the rise in sea-level). This process may be compared with the "bulldozing effect" involving ocean shelf areas where, after the LGM, huge masses of sands were pushed landwards by the rising sea-level (Cowell et al. 1992). In the case of Tapajós River, sands has been pushed from Rio Amazon into the Tapajós valley. Consequently, the sands at the base of the Tapajós core may slightly predate the Holocene and can be associated with the rapid rise in sea-level. This hypothesis is consistent with the age of the oldest clay-rich sediments in this sequence, which date to the start of the Holocene (ca. 11,000 years BP).

The initial phase of lake formation, characterized by a transition from a relatively high-energy environment to one of slack water, is evident at a depth of 42 m. The fine-grained sediment found exclusively above 38 m is representative of still-water lakes and is perhaps unexpected in "Lago Tapajós," where the average water discharge is 13,000 m^3 s^{-1}. The fine grain size can be explained by the sufficiently large volume of the lake, in which sediments did not collect within a principal channel. Additionally, the tide of the Atlantic Ocean reaches "Lago Tapajós" and, during slack water, conditions favor the deposition of extremely fine-grained sediments. What is evident from these data is that a relatively large lake filled the "Lago Tapajós" basin in the Holocene.

The mineral content of the sediments comprising the <2 μm fraction reflects sediment derived from a typical tropical soil surface. In warm wet settings, where clays weather easily, kaolinite, together with some Al-chlorite and gibbsite, dominates. The kaolinite is b-axis-disordered, as is the case in most surface horizons of Amazonian lowland soils. Quartz and illite are relicts of the primary geological formations of the drainage area, but siderite is formed in the lake or in its sediments. As for variations in clay minerals, no changes were observed in the entire section of the lake analyzed (Irion et al. 2006). The formation of siderite and the presence of relatively high concentrations of Fe and Mn are consistent with redox values in the deeper part of the water column and in the lake sediments. As the lake stabilized and deepened, these values decreased to those measured in modern times (Irion et al. 2006).

The vegetation during the phase of lake formation was characteristic of closed-canopy lowland forest with an abundance of riparian forest (e.g., *Cecropia, Ficus, Mauritia, Serjania*), marshland (*Alternanthera, Borreria*, Cyperaceae, *Ludwigia, Utricularia*), and terra firme elements (*Alchornea, Brosimum*-type, *Pouteria, Sapium, Sebastiana, Socratea, Symmeria, Waltheria*). Poaceae pollen was present in all samples and originated from wetland grasses, bamboos, or disturbed landscapes. A normal abundance range for Poaceae in várzea systems is 5–10%; the values observed here were a little higher than would be expected from a record of pure closed forest. Overall, the pollen record is consistent with a closed canopy forest and predicts sediments with strongly negative $\delta^{13}C$ values, as we have found (Fig. 2.10). Taken together, the flora, $\delta^{13}C$ values, and geochemistry do not provide evidence of biome change throughout the core, i.e., during the Holocene.

A significant climatic drying either at the base of the core or in the mid-Holocene region would have contained signatures of savannah expansion. In a dry climate resulting in savannah expansion, the soft surface material of the lowland would have been incised. This gully formation would have resulted in the erosion of soil horizons several decimeters or meters deep, where the composition of the material is significantly different from that of the surface. Kaolinite would be well-ordered instead of b-axis disordered, Al-chlorite, restricted to the upper few decimeters, would have become scarce or completely absent, and gibbsite concentrations would have decreased significantly (Irion 1984a). However, no such changes were evident in the core, from which we inferred that aridity did not play a major role in shaping the vegetation in this watershed during the last 11,000 years.

The most notable shift in the pollen record of the entire core occurs within a region corresponding to about 6,000 years BP. At this time, the abundance of *Cecropia* pollen is halved and that of Poaceae pollen doubled. This was most likely caused by human manipulation of the landscape although it cannot be excluded that increased seasonality increased the probability of dry-season fires or even centennial-/millennial-scale drought, causing the expansion of grasslands. However, the Poaceae pollen signature remains elevated to the present, making it unlikely that this change was due either to a mid-Holocene climatic event caused by an insolation peak or to a major drought. Furthermore, the lack of a consistent and substantial change in charcoal abundance along with the lack of change in the forest pollen component argues against a broad change in vegetation type.

By contrast, a change in the intensity of land use by humans as early as ca. 5,500 calender year BP is not unlikely in this setting (Bush et al. 2000), since archaeological sites in central Amazonia document at least 11,000 years of human occupancy (Roosevelt et al. 1991). The first evidence of long-term settlement and the adoption of ceramics came from 7,000-year-old middens located close to the modern city of Santarém. These sites, lying at the confluence of the Tapajós and the main Amazon channel, are within a few days walk of the shoreline adjacent to our coring site. That human occupation may have been quite widespread along the major river systems was suggested and authenticated by evidence of intensive pre-Columbian land use in the adjacent drainage of the Xingu (Heckenberger et al. 2003).

2.7 The Slope of the Amazon River Since the LGM

The variation in slope of the Amazon River may be regarded as an outstanding phenomenon in Quaternary history, one that induced far-reaching changes in river-current velocity as well as in sedimentation processes in the main valley and the lower section of the river's tributaries. Detailed studies of Ria lakes in Central Amazonia (Keim et al. 1999; Irion et al. 1999) and the eastern Amazon River (Irion et al. 2006) have allowed estimation of the variance in slope over the last

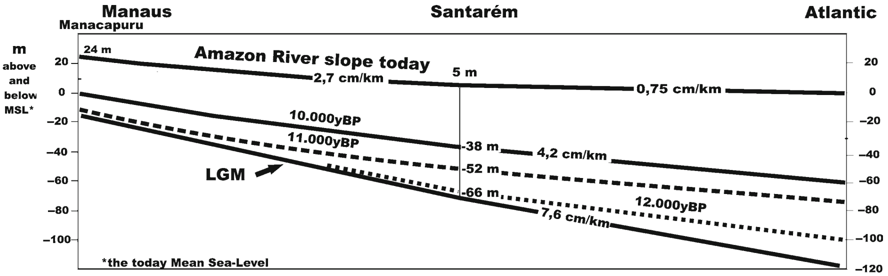

Fig. 2.11 Slope of the Amazon River since the Last Glacial Maximum (LGM), based on studies carried out in central Amazonia near Manaus and in the Tapajós River

20,000 years. In these studies, in which 3.5-kHz profiles of some of the smaller Ria lakes in Central Amazonia (Müller et al. 1995) and in the Negro River (Irion et al. 1999) along with profiles of the Tapajós River were obtained, the slope of the Amazon River during the LGM and at the start of the Holocene was measured. According to our results (Fig. 2.11), in the section between Manaus and Santarém the slope has decreased since the LGM from about 7.6 cm/km to about 2.7 cm/km, whereas between Santarém and the river mouth there has been a decrease from 7.6 to 0.75 cm/km.

Since high rainfall intensity is expected to have persisted during the entire Quaternary in most parts of the Amazon River watershed, the tenfold rise in slope must have dramatically affected the river floodplain system during the LGM. Kosuth et al. (2001) measured current velocity along the Amazon River and found maximum velocities of up to 3 m/s at Óbidos. This velocity is only reached by other large rivers during extreme floods. Most likely, the threefold to tenfold increase in slope during the LGM, assuming a similar water delivery, would have considerably increased the velocity of the water. However, much of the kinetic energy was probably absorbed by heavy erosion processes and sediment transport. In the pre-Andean zone, where there is high declivity, the tributaries of the upper Amazon displace their river beds with a velocity of up to 100 m/year (Salo et al. 1986). The middle and lower portions of the Amazon River have a rather stable river bed and floodplain. Most of the major hydromorphological structures have an age of several thousand years, as shown for the Marchantaria Island upstream of the confluence of Amazon and Negro Rivers (Irion and Junk 1989; Keim et al. 1999). We postulate that the Amazon River during the LGM was probably a braided river with a large very unstable floodplain. Thus, the turnover time of sediments deposited in the floodplain may have been reduced to centuries or even decades. Nonetheless, these time periods were sufficiently long to permit survival of the species-rich floodplain forest. Early successional stages, which developed over a few decades, may have prevailed but late successional stages, requiring several centuries, also occurred thereby maintaining the high species diversity that today characterizes Amazonian river-floodplain forests.

2.8 Discussion and Conclusions

From a geological point of view, there is no evidence for the occurrence of a significant dry climate period in central Amazonia during the last 10 million years (Irion 1978, 1984a, 1984b; Colinvaux et al. 2001). Based on analyses of the 42-m core from Rio Tapajós (Irion et al. 2006), we were unable to verify the occurrence of a dry period in the Amazonian lowland similar to the one that Absy et al. (1991) described for the Serra dos Carajás. Studies by Mayle et al. (2000) and Baker et al. (2001) also provided evidence of dry periods at the rim and outside the Amazonian lowland (Fig. 2.12). The paleoecological record from the core (Irion et al. 2006), representative of the last 11,000 years, indicates the continuous presence of a mesic forest landscape around "Lago Tapajós." On a landscape level, there were no substantial biome changes within the Holocene. While Holocene drying was strong enough to desiccate shallow lake systems, as documented in southeastern and southwestern Amazonia (Absy et al. 1991; Mayle et al. 2000), those records may have been more sensitive

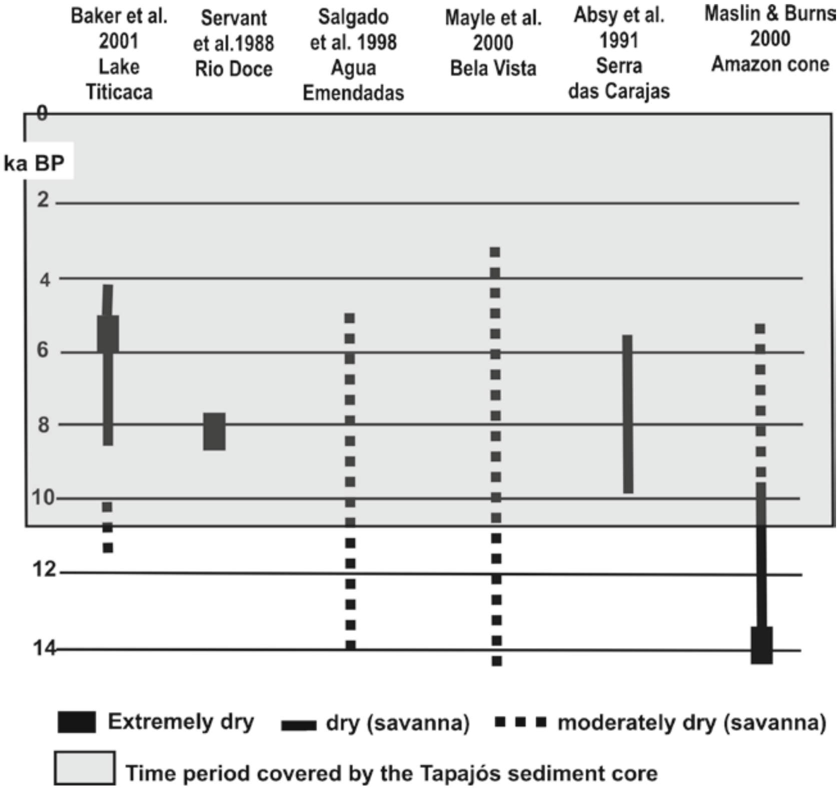

Fig. 2.12 The occurrence of dry periods during the Holocene, as suggested by various authors, is not supported by results obtained from the Tapajós sediment core

to local variations. The data of the sediment core obtained from the Tapajós River, by contrast, describe the largest part of the eastern Amazonian lowlands. The results are consistent with: (1) variations in the rise in sea-level as early as 11,000 BP, and (2) intensified human occupation of the lower Tapajós area from ca. 5,500 BP (Fig. 2.10).

It can be concluded that, at least in its largest parts during long periods of the Tertiary and throughout the Quaternary, the Amazon lowland was dominated by humid conditions. The waters of the Amazon River, which today course from the Andes to the Atlantic Ocean, formed during the Miocene, about 8 million years ago. Thereafter, the most characteristic event with respect to the aquatic system was the Mid-Pleistocene Revolution, when the huge ice shields of Laurentia (Canada) and Fennoscandia (Norway, Sweden, and Finland) penetrated many hundreds kilometers to the south and the sea-level dropped more than 100 m. At that time, the deeply incised Amazonian drainage system was created, giving rise to all the Ria lakes and the extremely large floodplain of the Amazon River.

The paleo-várzeas, first described by Irion 1976a, are still insufficiently analyzed. Physical data regarding their age are lacking, underlining the need for much more field and laboratory work.

Chapter 3
Remote Sensing of the Distribution and Extent of Wetlands in the Amazon Basin

John M. Melack and Laura L. Hess

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Abstract Basin-wide mosaics of synthetic aperture radar (SAR) data, validated with airborne videography, were used to map the extent and distribution of Amazonian wetlands. Cover states consisted of classes determined by vegetation physiognomy (non-vegetated, herbaceous, shrub, woodland, and forest) and by inundation state (flooded or non-flooded). About one-fourth of wetlands are in the Madeira basin. Large wetland features occur in the Marañón (Marañón-Ucayali palm swamps), Negro (Roraima savanna; Negro-Branco interfluvial wetlands), and Madeira (Llanos de Moxos) basins. The mainstem Amazon floodplain, with less than 2% of the total basin area, accounts for about 12% of the basin's wetlands. Basin-wide, about three-fourths of wetlands are covered by forest, woodland or shrubland. All large watersheds west of the Negro are at least 85% forested. The Madeira basin has the highest percentage of herbaceous wetlands. Numerous remote sensing studies of wetlands using SAR, passive microwave and optical data for selected areas that complement these basin-wide values are summarized.

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3.1 Introduction

Wetlands cover extensive areas in the Amazon basin and are represented by a wide variety of plant communities including seasonally inundated forests and savannas, intermittently flooded riparian zones bordering streams and rivers, backwater swamps, coastal mangroves, palm swamps, and high-elevation bogs (Junk 1997b). However, these wetlands are not well characterized, relative to their ecological importance. A major factor contributing to the difficulty of inventorying and monitoring the wetlands and their environmental functions has been the lack of means of determining their distribution and extent throughout the very large Amazon basin and the seasonal and interannual variations in their inundation and phenology.

The last two decades has seen development of a new suite of optical and microwave remote sensing systems and analysis algorithms that are advancing the understanding of wetlands (Melack 2004). However, a major challenge in the application of remote sensing to the study of wetlands is the large temporal and spatial scale of variation typical of wetlands (Sahagian and Melack 1998). An especially promising approach in humid tropical environments is synthetic aperture radar (SAR). Although the ability of SAR to detect inundation has been known for over 30 years (Hess et al. 1990), implementation of its ability was limited by lack of readily available data and algorithms appropriate for examination of wetlands. Within the last decade, techniques have been developed for accurately classifying digital radar images into vegetative classes and inundation status based on airborne and Space Shuttle-borne imaging radar (Hess et al. 1995; Wang et al. 1995; Kasischke et al. 1997). With the advent of satellites with SAR sensors, monitoring of inundation and wetland vegetation has become feasible.

3.2 Overview of Wetlands Within the Amazon Basin

Vegetative cover of wetlands within the Amazon basin varies as a function of hydrologic regime, topography, soils, and the optical and nutritional properties of the waters (Prance 1979; Salo et al. 1986; Junk 1993, 1997a; Junk and Furch 1993; Klinge et al. 1990). The large rivers usually have unimodal annual floods that last for several months and inundate extensive floodplains covered by open water, flooded forests and aquatic macrophytes. The waters vary from sediment-laden, white-water rivers (e.g., Amazon, Madeira, Purus, Juruá and Japurá) rich in dissolved nutrients to the relatively sediment-free black-water rivers (e.g., Negro) with high dissolved organic carbon and low levels of nutrients and other solutes, to clear-water rivers (e.g., Tapajós and Xingu) that tend to be intermediate in sediment load and solute content. Smaller rivers and streams display polymodal inundation of their narrow fringing floodplains, but over one million kilometers of these habitats lead to their regional importance. In portions of the basin with a pronounced dry season, savannas occur and are exposed to seasonal flooding from local rain and rivers (e.g., Roraima in Brazil and Llanos de Moxos in Bolivia). Poorly drained Spodosols cover considerable areas, and their acidic and nutrient-poor waters can support flooded *caatinga* vegetation. Extensive wetlands covered by nearly monospecific stands of palms, including *Mauritia flexuosa* and *Copernicia alba*, occur in the upper Negro River in Colombia, the upper Amazon in Peru, and the Llanos de Moxos.

Junk and Piedade (2005) provide a preliminary classification of Amazonian wetlands and note that the areas that they estimate as covered by each category are rough estimates and that remote sensing techniques are likely to considerably improve the estimates. Many studies have focused on wetland vegetation of the Brazilian Amazon, particularly on floodplains of the mainstem Amazon and large white-water tributaries (Campbell et al. 1992; Worbes et al. 1992; Ayres 1993; Junk and Piedade 1993; Junk 1997a; Junk and Ohly 2000; Wittmann et al. 2004) and of the Negro River and its tributaries (Keel and Prance 1979; Revilla 1981; Ferreira 2000). Vegetation communities of the extensive and diverse wetlands of the Bolivian Amazon are described in detail in volumes by Navarro and Maldonado (2002) and Pouilly et al. (2004). Kvist and Nebel (2001) present a key to 16 wetland habitat types of Peruvian floodplains based on the classification system of Encarnación (1993), and review the considerable literature focused on these wetlands, which has emphasized the importance of fluvial dynamic processes and successional stage (Lamotte 1990; Kalliola et al. 1991; Puhakka et al. 1992) and of palm communities (Kahn and Mejia 1990). Wittmann et al. (2006a) compare species composition of white-water floodplain forests of Amazonia across a broad latitudinal gradient.

3.3 Remote Sensing Applied to Amazon Wetlands

Optical and microwave remote sensing instruments detect distinct sets of characteristics of wetland environments, and thus are highly complementary in their capabilities (Hess and Melack 1994; Melack et al. 1994). Optical sensors such as Landsat Thematic Mapper are useful for mapping wetland vegetation type (Brondizio et al. 1996; Novo and Shimabukuro 1997; Wittmann et al. 2002b), fluvial dynamics (Kalliola et al. 1992; Mertes et al. 1995; Charriére et al. 2004), and water properties (Mertes et al. 1993; Barbosa 2005; Rudorff et al. 2006). However, observations with optical remote sensing are frequently impeded by cloud cover or smoke in Amazonia (Asner 2001), precluding the monthly or better temporal resolution required to document seasonally varying inundation and plant phenology. Furthermore, many floodplain forest canopies are too dense to allow detection of flooding. Alternatively, passive and active microwave systems, which are much less influenced by clouds and smoke and can penetrate vegetation at some wavelengths, have been employed to detect the presence of surface water (Sippel et al. 1994; Hess et al. 1995; Hoekman and Quiñones 1998; Martinez and Le Toan 2007) and, in the case of SAR, to characterize the vegetative structure (Costa et al. 1998; Moreau and Le Toan 2003; Costa 2005).

The ability to map wetland extent and properties over large regions at a spatial resolution on the order of 100 m or higher requires mosaicking of hundreds or thousands of scenes, assuming availability of the datasets. In the past decade, sufficient imagery has been acquired to produce high-resolution mosaics of the Amazon basin from both optical and microwave imagery. Here we highlight studies that have examined the extent and distribution of Amazonian wetlands using such mosaics, with emphasis on analysis of the mosaics of JERS-1 (Japanese Earth Resources Satellite-1) data produced by the Global Rain Forest Mapping Project (Rosenqvist et al. 2000; Siqueira et al. 2000; Chapman et al. 2002).

Studies carried out using high-resolution Landsat mosaics of the Peruvian Amazon illustrate two approaches to mapping and characterizing wetland habitats using optical data, one based primarily on the spatial characteristics of open water areas (Toivonen et al. 2007) and one primarily on the spectral characteristics of vegetation (Biodamaz 2004; Josse et al. 2007). Based on a mosaic of 128 Landsat Thematic Mapper (TM) scenes acquired from 1987–1996 and resampled to 100 m, Toivonen et al. (2007) used the TM5/TM2 band ratio to map open water areas over a 2.2 million km^2 portion of the western Amazon. Open water bodies over 1 ha in size or 60 m in width were found to cover 1.1% of the area. GIS-based analysis was then employed to classify rivers based on channel properties, categorize lakes according to size and relation to river type, and define riverine corridors, which covered 17% of the land area. Based on these features, three major fluvially distinct regions were identified.

At least 12 wetland types were found to be identifiable on a Landsat TM mosaic of the lowland Peruvian Amazon collected during the 1980–2000 period (Biodamaz 2004), including types distinguished by particular species such as aguajales (*Mauritia flexuosa*), renacos (*Ficus* sp. and *Coussapoa* sp.), and pacales (*Guadua* sp. and *Merostachys* sp.). In a more extensive study, Landsat TM mosaics were the primary data set used in mapping ecological systems of the eastern Andean foothills and adjacent Amazonian plains of Bolivia and Peru at a scale of 1:250,000 (Josse et al. 2007). Factors such as bioclimate, geomorphology, and phytogeographic regions were combined with vegetation characteristics, resulting in 84 mappable ecological systems for the 1.25 million square kilometers area. The 40 mapped wetland systems are grouped into four major subdivisions of Amazonian wetlands (white-water floodplain forests, black-water floodplain forests, Amazonian clear-water floodplain forests, and white- or black-water flooded vegetation), and three of Bolivian wetlands (Beni seasonally saturated vegetation, Beni seasonally flooded vegetation, and Beni permanently flooded vegetation), each subdivision in turn containing two to nine ecological systems (e.g., Subandean palm swamp of the Yungas, Central-south Amazon black-water floodplain forest, Beni seasonally flooded herbaceous mesotrophic savanna). Flooded and poorly drained systems covered 27.7% of the Amazonian lowlands region.

The mosaicking of SAR images of the Amazon acquired by the Japanese Earth Resources Satellite-1 (JERS-1) during low and high water stages (Chapman et al. 2002) has made possible, for the first time, basin-wide delineation of wetland area and vegetative structure. Hess et al. (2003) have developed a wetlands mask and a classification of vegetative-hydrologic state using the JERS-1 mosaics and have validated these products using high-resolution digital videography (Hess et al. 2002). Four aerial videographic surveys were conducted to acquire data sets suitable for training of classification algorithms and assessment of accuracy.

The first step in wetlands mapping using the radar mosaics was creation of a wetlands mask, a binary classification denoting wetland and non-wetland areas (Hess et al. 2003). Wetlands were defined as (1) areas that were inundated during either or both JERS-1 mosaic acquisition periods; and (2) areas not flooded on either date, but which were adjacent to or surrounded by flooded areas and which displayed landforms consistent with wetland geomorphology. Creation of a wetlands mask permitted calculation of total inundated area and eliminated from the classification process non-wetland areas. Wetland extent was delineated with an overall accuracy of 95%.

Following wetlands delineation, areas within the wetlands mask were classified into cover states for both seasons. Cover states consisted of classes determined by vegetation physiognomy (non-vegetated, herbaceous, shrub, woodland, and forest) and by inundation state (flooded or non-flooded). Shrubs were defined as woody plants with multiple stems, which lack definite crowns and are less than 5 m tall; woodlands were defined to have less than 60% canopy cover. This vegetative-hydrologic classification scheme meets the criteria for a "functional parameterization" of wetlands (Sahagian and Melack 1998), with classes suitable for biogeochemical modeling of wetland functions, and is useful for ecoregion designation to aid biodiversity assessments (Pressey et al. 2005). Using the methodology developed for the central Amazon, the JERS-based mapping of wetland areas was extended to the lowland Amazon basin (Melack and Hess 2004).

Satellite-borne passive microwave sensors can record patterns of seasonal inundation in large floodplains and wetlands (Sippel et al. 1994). Sippel et al. (1998) determined seasonal and interannual variations in inundation for the mainstem Solimões/Amazon floodplain in Brazil based on an analysis of the 37 GHz polarization difference observed by the Scanning Multichannel Microwave Radiometer (SMMR) on the Nimbus-7 satellite. The algorithms were developed and calibrated by drawing on multiple sources of information on geomorphology, vegetation and inundation, and the results were validated by comparison with river stage records. Hamilton et al. (2002) applied a similar approach to the Llanos de Moxos in Bolivia, the Bananal in Brazil, and Roraima savannas in Brazil and Guyana.

3.4 Regional Extent of Floodplains and Aquatic Habitats

Prior estimates – Global land cover maps include the Amazon basin but are not well designed to determine wetlands. Two global 1 km land cover datasets derived from 1992 to 1993 Advanced Very High Resolution Radiometer data are the DISCover (Loveland et al. 2000) and the University of Maryland (Hansen et al. 2000) maps. The University of Maryland product does not include wetlands. The DISCover approach was not suited to detection of wetlands; hence wetlands are under-represented in the database and only about 6,000 km^2 of permanent wetlands are listed for the South American continent. Based on a comparison among three global wetland inventories and Ramsar data, Darras et al. (1999) noted large differences in total wetland areas, little spatial fidelity among the inventories and concluded that all are underestimates. Lehner and Döll (2004) developed a global lakes and wetlands database based on a variety of existing maps and other information; their wetland area for the Amazon basin is 357,000 km^2.

Saatchi et al. (2000) approximated a land cover map of the Amazon basin at 1 km resolution based on the JERS-1 mosaic developed by Siqueira et al. (2000). They used a 1:2,500,000 map of vegetation for supervising the classification. No areal estimates of wetland types (i.e., seasonally flooded forests, riverine shrublands, riverine palm swamps, herbaceous plants) delineated on the map were provided.

Based on geomorphological maps produced by RADAM (e.g., Projeto RADAMBRASIL 1978), Junk (1997a) determined the floodplain areas for the large Amazonian rivers in Brazil. The floodplain area for the Solimões/Amazon from the Peru/Colombia border to the mouth of the Xingu River was estimated as 87,600 km^2 or 107,700 km^2, if floodplains of minor affluents are added. The total for all the rivers was estimated as 203,100 km^2 or 307,300 km^2, if floodplains of minor affluents are added.

Throughout the Amazon basin, hydromorphic or water-logged soils and frequently flooded riparian zones along the numerous streams add considerable area where wetlands plants and biogeochemical processes are likely to occur. For example, Junk (1993) reported a stream density of 2 km of stream channel per square kilometers and about 40% hydromorphic soils north of Manaus in the central Amazon. If extrapolated basin-wide, several hundred thousand square kilometers of such environments occur.

Current regional estimates derived from remote sensing – Recent remote sensing of the extent of wetlands in the Amazon has well defined geographic boundaries such that wetland distribution as well as areal coverage can be documented unambiguously. Studies have been conducted from the mesoscale to basin-scale. While only broad classes of vegetation can be deciphered, seasonal and interannual variations in inundation and vegetative cover add important information. Since the composition and phenology of the vegetation are strongly linked to the frequency, amplitude and depth of inundation, recent advances in inundation hydrology are relevant here.

Inundation extent and vegetation under low and high water conditions at 100 m resolution were mapped for a 1.77 million square kilometers quadrant (18° × 8°) in the central Amazon (Hess et al. 2003). Stage heights at Manaus on the JERS-1 mosaic imaging dates were 27.97 m for the high-water mosaic (0.36 m higher than the mean for 1903–1999) and 15.36 m for the low-water mosaic (3.00 m lower than the long-term mean). The mapped conditions can thus be seen as representative of typical high-water conditions and below-normal low-water conditions; the mean recurrence interval for a low of 15.36 m is 10 years. Seventeen percent of the quadrant was identified as wetland, of which 96% was inundated at high water and 26% was inundated at low water. While flooded forest occupied nearly 70% of the wetlands at high water, aquatic habitats varied regionally as a function of geomorphology and environmental conditions.

To estimate the monthly variations in inundation for the 1.77 million square kilometers quadrant in the central Amazon, Richey et al. (2002) combined analyses

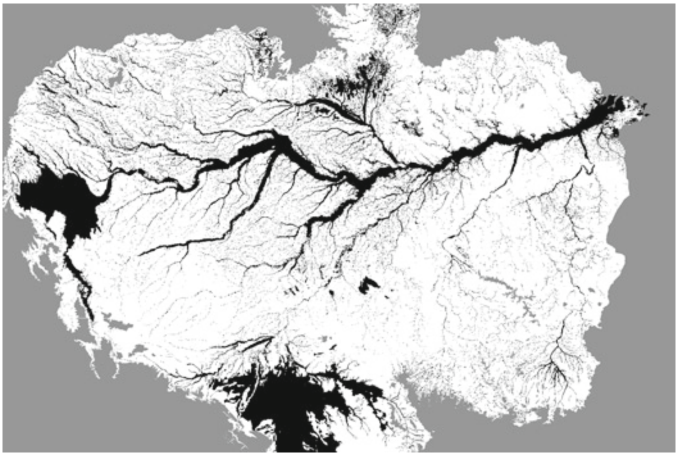

Fig. 3.1 Floodable area (*black*) for Amazon basin below 500 m contour derived from JERS synthetic aperture radar mosaic. Floodable areas are not all inundated simultaneously and may include areas not floodable that do not appear on the scale of the figure

of the JERS-1 mosaic for rivers larger than about 100 m wide (Hess et al. 2003), passive microwave data for the mainstem Amazon and its floodplain (Sippel et al. 1998) and mean monthly river stage data from tributaries to approximate the temporal flooding patterns for these rivers. To account for river corridors less than 100 m in width, an area-stream density function was computed from a digital river network and extrapolated to the smaller rivers (Mayorga et al. 2005). The summation for all rivers and floodplains plus estimates for small rivers and streams results in the region being most flooded in May with 350,000 km^2 inundated, or 20% of the quadrant.

Applying the same approach to delimit floodable area as used by Hess et al. (2003) to whole lowland Amazon basin (the region less than 500 m above sea level) results in a map of floodable area at 100 m resolution (Fig. 3.1). Total floodable area within the low-land basin is about 800,000 km^2, or 14% of the entire area. The actual floodable area is larger, since areas in southern Bolivia and high-altitude wetlands were not included in the JERS-based mapping, and floodplains in the southwestern Brazilian Amazon were not well delineated owing to the timing of the mosaics. In addition, floodplains of small but very numerous low-order streams, and small interfluvial wetlands, could not be mapped at the ~100 m resolution of the SAR mosaics.

The regional distribution of wetlands (floodable areas, including river channels and lakes) by hydrographic unit is detailed in Table 3.1. The delineation of hydrographic regions (Fig. 3.2) modifies watershed schemes, such as that of Mayorga et al. (2005), by considering the mainstem Amazon floodplain as a separate unit. Watersheds were derived from the Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) at 15 arcsec resolution using the RiverTools software package,

Table 3.1 Wetland area and vegetation cover for hydrographic sub-units of the Amazon basin (see Fig. 3.2). For several hydrographic units the basin boundaries extend beyond the region included in our analysis, hence the mapped areas are less than the whole area

		Total area		Floodable area[a]		Vegetation cover		
		Whole	Mapped	Mapped	Percent of mapped area floodable	Water/bare	Herbaceous	Woody
Hydrographic unit	No.	Thousands of km²		Thousands of km²		Percent of floodable area		
Madeira	9	1,316.6	1,057.4	210.1	19.9	5.8	33.5	60.7
Negro	25	712.4	685.1	119.6	17.5	7.8	7.4	84.8
Tapajós	6	492.6	492.5	22.4	4.5	21.1	1.4	77.6
Xingu	3	491.9	491.9	37.1	7.5	8.6	1.0	90.4
Purus	11	368.4	368.2	36.1	9.8	3.4	5.6	91.0
Marañón	19	358.3	287.2	71.0	24.7	1.6	5.0	93.4
Ucayali	18	356.4	356.3	41.5	11.6	3.8	5.5	90.6
Japurá-Caquetá	23	255.9	255.9	31.9	12.5	6.8	6.2	87.0
Juruá	14	189.5	189.3	20.9	11.0	2.4	6.8	90.7
Trombetas	28	119.1	119.1	7.4	6.2	7.3	1.6	91.1
Içá-Putumayo	22	118.2	117.9	20.3	17.2	5.1	4.0	91.0
Abacaxis	8	112.6	112.4	8.2	7.3	16.1	1.8	82.1
Javari-Yavari	17	107.5	107.5	5.4	5.0	0.5	5.2	94.3
Napo	21	102.1	99.4	10.7	10.8	6.9	6.6	86.5
Mainstem floodplain[b]	1	98.2	98.1	95.1	96.9	21.2	9.7	69.1
Jutaí	15	75.3	75.0	8.1	10.8	1.8	5.6	92.6
Uatumã	26	69.5	69.5	6.3	9.1	8.8	3.3	87.8
Madeirinha	10	39.7	39.7	6.0	15.1	7.3	1.5	91.2
Paru d'Este	31	38.8	38.8	1.8	4.5	1.9	2.0	96.1
Coari	12	35.4	35.4	4.0	11.3	19.3	0.6	80.1
Curuá-una	5	31.2	31.0	0.7	2.3	4.1	2.8	93.0
Nhamundá	27	26.6	26.6	1.6	6.1	16.6	2.7	80.7
Curuá	29	29.7	29.4	1.3	4.4	0.4	0.5	99.0
Tefé	13	24.1	24.1	2.8	11.7	10.0	0.5	89.5

Nanay	20	16.7	16.5	1.9	11.3	0.1	3.1	96.8
Jarauçu	4	15.3	15.0	0.6	4.0	1.2	1.5	97.2
Maicuru	30	15.0	14.7	0.5	3.7	2.8	1.2	96.0
Jandiatuba	16	14.1	14.0	0.9	6.1	0.2	9.2	90.6
Piorini	24	10.2	10.2	2.0	19.2	17.1	0.7	82.3
Mamuru	7	10.1	10.0	0.7	6.8	28.1	4.1	67.8
Aggr. small basins[c]	2	171.7	171.7	22.0	12.8	8.8	1.9	89.3
Basin total[d]		5,819.7	5,459.6	798.9	14.6	8.1	13.0	78.9

[a] Floodable area mapping based on ~100 m radar mosaics; floodplains <~150 m wide are not included

[b] Floodplain of Amazonas-Solimões-Amazonas river between Marañón-Ucayali confluence and Gurupá Island

[c] Aggregate area of basins <10,000 km^2 draining directly to mainstem floodplain

[d] Basin delineation excludes Marajó Island and Amazon estuary

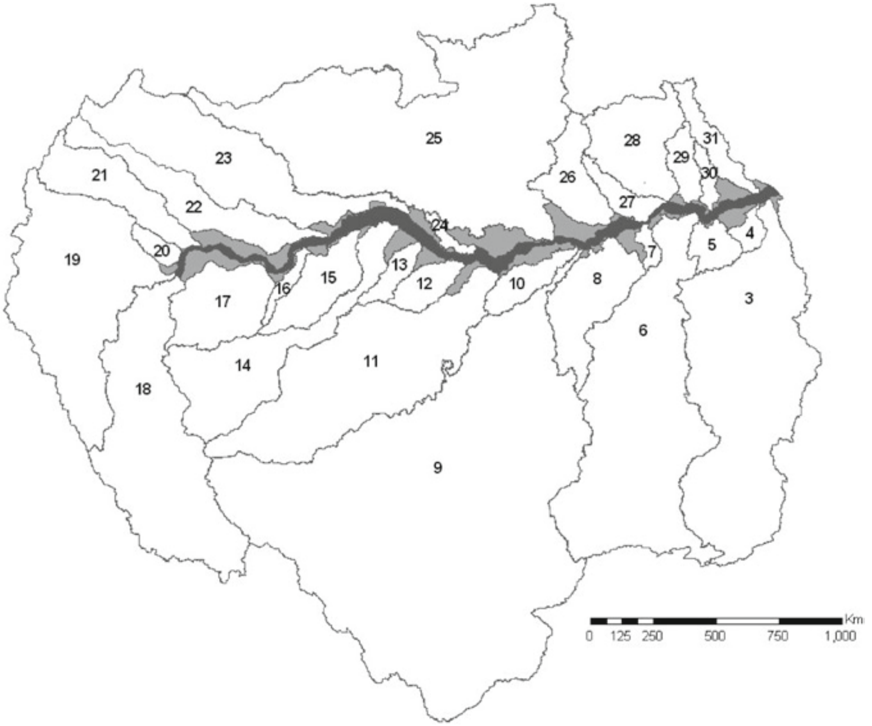

Fig. 3.2 Hydrographic sub-units of the Amazon basin: Mainstem floodplain (1; *dark gray*), aggregated mainstem tributaries <10,000 km^2 (2; *light gray*), Xingu (3), Jarauçu (4), Curuá-una (5), Tapajós (6), Mamuru (7), Abacaxis (8), Madeira (9), Madeirinha (10), Purus (11), Coari (12), Tefé (13), Juruá (14), Jutaí (15), Jandiatuba (16), Javari-Yavari (17), Ucayali (18), Marañón (19), Nanay (20), Napo (21), Içá-Putumayo (22), Japurá-Caquetá (23), Piorini (24), Negro (25), Uatumã (26), Nhamundá (27), Trombetas (28), Curuá (29), Maicuru (30), and Paru d'Este (31)

and setting the basin outlet west of Gurupá Island (approximately 51.4375°W, 0.4583°S) where the mainstem Amazon channel splits into north and south channels. The mainstem floodplain was digitized from the Marañón-Ucayali confluence to the basin outlet using the JERS-1 mosaics, based on a combination flooding extent and geomorphologic features. The resulting floodplain outline closely parallels areas designated in RADAM maps of Brazil (e.g., Projeto 1978) as Apf (fluvial plain) or Apfl (fluvio-lacustrine plain). Watersheds tributary to the mainstem were truncated to terminate at the edge of the mainstem floodplain rather than extending to the channel. All basins with areas greater than 10,000 km^2 are listed in Table 3.1. Basins smaller than 10,000 km^2 are listed together as "Aggregate small basins". The total basin area of 5,821,800 km^2 is smaller than that given by some sources since it does not include Marajó Island, the Amazon estuary, or the Jari watershed. Areas for tributary basins are smaller than those given elsewhere since the portion extending across the mainstem floodplain is not included.

As can be seen in Table 3.1, the distribution of wetlands throughout the basin is heterogeneous with some regional trends. About one-fourth of wetlands are in the Madeira basin. Nearly all the basins with less than 10% floodable area are in the eastern Amazon. The effect of large wetland features is reflected in high percent floodable area for some of the large watersheds (>100,000 km^2), for example the Marañón (Marañón-Ucayali palm swamps), the Negro (Roraima savannas; Negro-Branco interfluvial wetlands), and the Madeira (Llanos de Moxos). The mainstem floodplain, which constitutes less than 2% of the total basin area, accounts for about 12% of the basin's wetlands. About 97% of the mainstem floodplain is mapped as floodable; the remaining 3% consists of small outliers of non-floodable terrain, including Pleistocene várzeas, within the floodplain proper. Basinwide, about three-fourths of wetlands are covered by forest, woodland, or shrubland (Table 3.1). All large watersheds west of the Negro are at least 85% forested. The Madeira basin has the highest percentage of herbaceous wetlands, corresponding to the Llanos de Moxos and other savanna wetlands of the Beni, Madre de Dios and Guapore rivers.

For the mainstem floodplain, timing of the JERS-1 acquisitions closely approximated typical high-water and below-normal low-water conditions (Hess et al. 2003). Detailed information on flooding and vegetation cover for high- and low-water conditions based on the mosaics is shown in Table 3.2 for five geomorphic sub-units of the mainstem floodplain. Subdivision of the mainstem (Fig. 3.3) is based on broad topographic highs of varying origin (Wesselingh and Salo 2006) but usually referred to as arches. These arches have been shown to influence hydro-geomorphic processes and patterns including channel-floodplain sediment exchanges, channel width and radius of curvature, and number and shape of floodplain lakes (Mertes et al. 1995; Dunne et al. 1998). Because such factors shape floodplain topography and help determine inundation periodicity and vegetation, these geomorphic subdivisions are an appropriate spatial stratification of the floodplain for ecological and biogeochemical studies. Locations of the structural highs are imprecise, vary between sources and are mapped at low resolution. The subdvisions here correspond closely to maps of Dunne et al. (1998) and Roddaz et al. (2005), adjusted to fall at tributary confluences so as to be more easily comparable with other datasets. The five sub-units are (1) Marañón to Nanay; (2) Nanay to Jandiatuba; (3) Jandiatuba to Purus; (4) Purus to Tapajós; (5) Tapajós to channel bifurcation west of Gurupá Island. The downstream boundaries of the units correspond, respectively, to the Iquitos Arch, Carauari or Jutaí Arch, Purus Arch, Monte Alegre Arch/Intrusion, and Gurupá Arch.

At high water stage, 84,430 km^2, or 86% of the total mainstem floodplain area of 98,110 km^2, was flooded, while 45% (43,930 km^2) was flooded at low water stage (Table 3.1). Extent of flooding at high and low water varied considerably: for segments 1, 2, 3, 4, and 5, high-water flooding occupied 60%, 80%, 86%, 92%, and 89% of the segments, respectively, and low-water flooding occupied 34%, 29%, 30%, 54%, and 68%. Flooded extent includes permanent channels and lakes. In Fig. 3.4, regional differences can be seen in the proportion of the floodplain occupied by forest. The three upstream segments are primarily forested, while along the two

Table 3.2 Vegetative cover and flood extent at high and low water stages for geomorphic sub-units of the mainstem Amazon floodplain. Five floodplain segments (see Fig. 3.3) are defined by river confluences corresponding to structural features

	1	2	3	4	5	
	Marañón to Nanay	Nanay to Jandiatuba	Jandiatuba to Purus	Purus to Tapajós	Tapajós to Gurupá	Main-stem total
	km^2 × 10^3	km^2 × 10^3	km^2 × 10^3	km^2 × 10^3	km^2 × 10^3	km^2 × 10^3
High water stage[a]						
Flooded						
Open water	0.35	2.27	3.87	11.76	3.94	22.19
Aquatic macrophyte	0.11	0.68	1.84	4.92	2.33	9.88
Shrub	0.12	0.47	0.65	0.96	0.29	2.49
Woodland	0.29	0.82	1.29	2.1	2.05	6.55
Forest	0.98	13.26	20.58	6.76	2.06	43.65
Total flooded	1.85	17.49	28.23	26.51	10.68	84.76
Non-flooded						
Bare ground	0	0	0	0	0	0
Herbaceous	0	0	0	0	0	0
Shrub	0	0	0	0	0	0
Forest	0.9	2.76	3.71	1.8	1.11	10.28
Total non-flooded	0.9	2.76	3.71	1.8	1.11	10.28
Floodable[b]	2.75	20.25	31.94	28.31	11.79	95.04
Non-floodable[c]	0.29	1.55	0.71	0.43	0.09	3.07
Total area	3.04	21.8	32.65	28.74	11.88	98.11
Low water stage[a]						
Flooded						
Open water	0.32	2.04	2.92	8.8	3.41	17.49
Aquatic macrophyte	0.05	0.4	1.22	3.08	1.54	6.3
Shrub	0.04	0.14	0.06	0.13	0.07	0.44
Woodland	0.29	0.82	1.29	2.1	2.05	6.55

Forest	0.37	3	4.26	1.45	1	10.08
Total flooded	1.07	6.4	9.75	15.57	8.07	43.93
Non-flooded						
Bare ground	0.05	0.33	1.22	3.64	0.89	6.14
Herbaceous	0.12	0.5	0.95	1.99	0.65	4.21
Shrub	0	0	0	0	0	0
Forest	1.51	13.03	20.02	7.11	2.17	43.84
Total non-flooded	1.68	13.86	22.19	12.74	3.71	54.18
Floodable[b]	2.75	20.25	31.94	28.31	11.79	95.04
Non-floodable[c]	0.29	1.55	0.71	0.43	0.09	3.07
Total area	3.04	21.8	32.65	28.74	11.88	98.11

[a] The mapped conditions correspond to typical high-water conditions and below-normal low-water conditions (27.97 m at Manaus gauge at high water, 15.36 m at low water) on imaging dates

[b] Sum of *Total flooded* and *Total non-flooded*; the area that would be flooded at extreme (not average) high water stage

[c] *Non-floodable area*: small inclusions of areas not subject to flooding

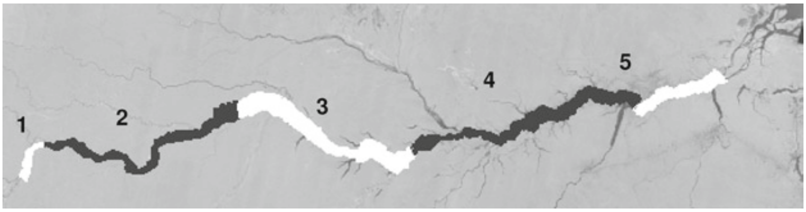

Fig. 3.3 Geomorphic sub-units of Amazon mainstem floodplain based on structural highs (Dunne et al. 1998; Roddaz et al. 2005). Sub-unit boundaries are located at tributary confluences adjacent to approximate arch locations. (1) Marañón to Nanay; (2) Nanay to Jandiatuba; (3) Jandiatuba to Purus; (4) Purus to Tapajós; and (5) Tapajós to channel bifurcation west of Gurupá Island

downstream segments most forest cover is replaced by open water or aquatic macrophytes (shown as flooded herbaceous in Fig. 3.4).

Time series of SAR data at three or 6 week intervals are available for several subregions within the Amazon basin and can be used to generate high-resolution maps of wetlands and their seasonal variations. Martinez and Le Toan (2007) used a time series of JERS-1 SAR images to map temporal variations in inundation (distinguished as never, occasionally, or always flooded) and the spatial distribution of vegetation (distinguished as pastures or clear cuts, savannas or pioneer formations, forests) for the Curuaí floodplain near Santarém, Brazil. Aerial photographs, aerial videography, ground observations and a Landsat image were used to evaluate the accuracy of their map.

The Mamirauá Sustainable Development Reserve is located about 50 km upstream of the confluence of the Japurá and Solimões rivers and covers approximately 2,600 km^2 with most of the area covered by closed-canopy forests. Wittmann et al. (2002) combined field inventories of tree species distribution and abundance with aerial photography to characterize canopy status, and were able to distinguish low and high flooded forest using a supervised classification of a Landsat image. The borders of the low forest were difficult to determine, and early successional stages were too narrow for the 30 m spatial resolution.

The sub-Andean portion of the Amazon basin has exceptional biodiversity, in part, related to the fluvial geomorphology. To evaluate the capability of remote sensing to offer surrogates for biodiversity, Hamilton et al. (2007) examined a portion of the catchment of the Madre de Dios River in Peru. Optical data from Landsat, SAR data from JERS-1 and topographic data from the interoferometric SAR were integrated to distinguish five classes of floodplain vegetation. The vegetation classes tended to correspond to successional stages that reflected meandering of the river.

As part of an analysis to estimate the volume of water stored in the floodplains of the Negro River based on JERS-1 data, Frappart et al. (2005) produced a classification of the ca. 700,000 km^2 Negro basin that identified areas of occasionally flooded forests (79,700 km^2), occasionally flooded pastures and low vegetation (37,000 km^2) and permanently flooded forests (21,900 km^2). This classification was

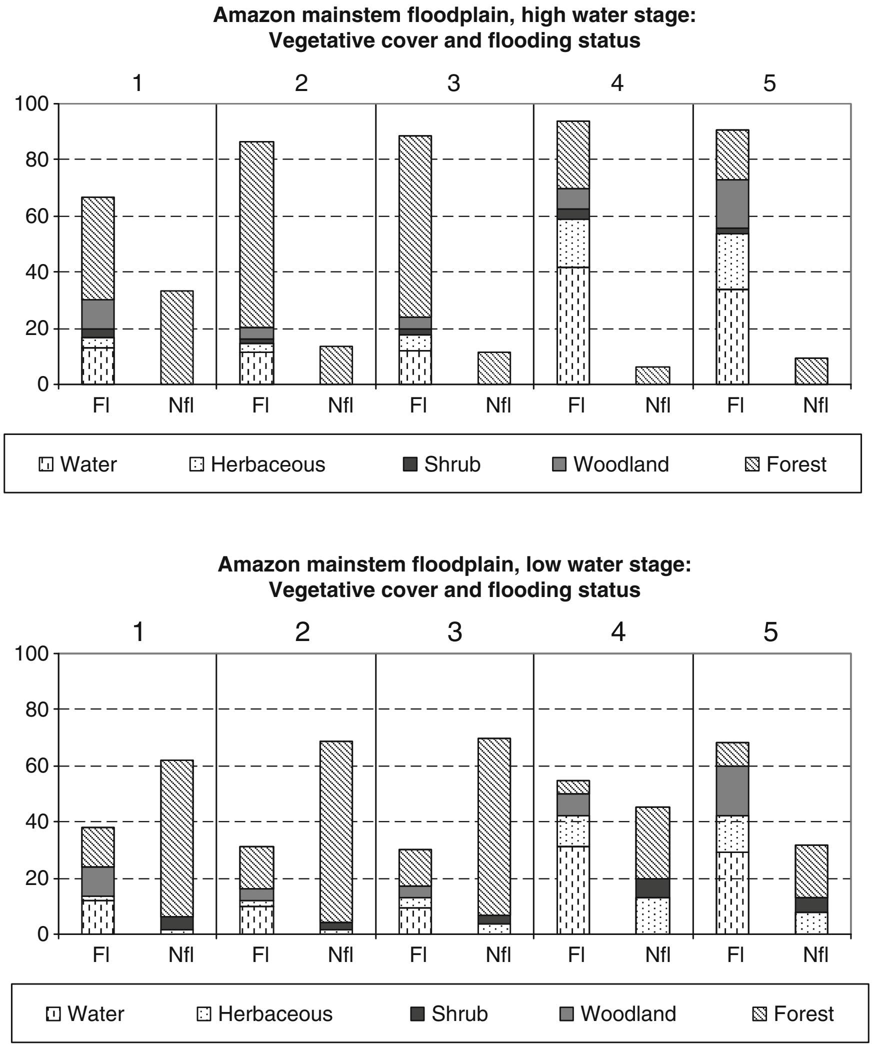

Fig. 3.4 Vegetative cover and flooding status for five segments of Amazon mainstem floodplain shown in Fig. 3.3, for high and low water conditions imaged on the JERS-1 mosaics (average high-water conditions and below-average low-water conditions; see text and Table 3.2). For each segment, percent cover of flooded (Fl) and nonflooded (Nfl) states of five cover types is shown. Bars represent percent of floodable area of each segment

checked against a site near Óbidos, but was not statistically validated. By utilizing the regional perspective offered by the JERS-1 mosaic, Forsberg et al. (2000) were able to identify evidence for tectonic control of the wetland distribution in the lower Negro basin.

While peatlands are often not considered significant in the lowland Amazon basin, Ruokolainen et al. (2001) combined information from satellite imagery, land cover maps, field observations and publication to offer "educated guesses" that there are approximately 55,000 km^2 of mires in Brazil, 50,000 km^2 in Peru, 10,000 km^2 in Colombia and 5,000 km^2 in Ecuador. Most of these mires are *Mauritia* swamps.

Satellite-borne passive microwave sensors provide a record of seasonal inundation in four large floodplains in the Amazon basin: mainstem Amazon River floodplain in Brazil, Llanos de Moxos (Beni and Mamoré rivers) in Bolivia, Bananal (Araguaia River) in Brazil, and Roraima savannas (Branco and Rupununi rivers) in Brazil and Guyana (Hamilton et al. 2002, 2004). The maximum areas subject to inundation (including open water in lakes and rivers) during an 8-year period (1979–1987) were as follows (in km^2): mainstem Amazon 97,400; Moxos 92,100; Bananal 58,600; Roraima 16,500. Total extent of inundation of these floodplains varied considerably seasonally and interannually, with the greatest relative variation in maximum extent of inundation in the Bananal and Roraima. Regressions between flooded area and stage heights in nearby rivers were used to extend the records of inundation for nearly a century for the Amazon mainstem and for several decades for the other floodplains.

A complementary approach to remote sensing of floodplain inundation is the combination of modeling and remote sensing. Basin-scale hydrological models that include floodplain inundation operate at moderate resolution (e.g., ~9 km, Coe et al. 2002; Coe et al. 2007) and provide monthly estimates of inundated area. Alsdorf et al. (2007) used interferometric SAR measurements from the JERS-1 satellite to document the passage of a flood through a large, topographically complex floodplain at the confluence of the Purus and Solimões rivers. They noted abrupt differences in stage changes coincident with floodplain channels and that spatial patterns were localized during mid-rising water compared to high-water conditions. By combining interferometric SAR measurements of stage changes and a continuity equation, Alsdorf et al. (2005) developed a linear diffusion model of floodplain drainage that captures the composite behavior of flow through channels, lakes and aquatic vegetation. In the first application and validation of two-dimensional hydrodynamic model to a large reach of Amazon floodplain, Wilson et al. (2007) found that more than 40% of the total river flow was routed through the floodplain near the confluence of the Purus and Solimões rivers.

3.5 Conclusions

The recent developments of a suite of optical and microwave remote sensing systems and analysis algorithms have advanced the understanding of Amazon wetlands, and application of synthetic aperture radar (SAR) is especially useful. The advent of satellites with SAR sensors has made the regional and time-series analyses of inundation and wetland vegetation feasible. For example, mosaicking of SAR images of the Amazon acquired by the Japanese Earth Resources Satellite-1 (JERS-1) during low and high water stages has made possible, for the first time, basin-wide delineation of wetland area and vegetative structure. Cover states consisted of classes determined by vegetation physiognomy (non-vegetated, herbaceous, shrub, woodland, and forest) and by inundation state (flooded or non-flooded).

Remote sensing of the extent of wetlands in the Amazon has well defined geographic boundaries such that wetland distribution as well as areal coverage can be documented unambiguously. Such studies have been conducted from the mesoscale to basin-scale. Total floodable area within the lowland basin (the region less than 500 m above sea level) at 100 m resolution is about 800,000 km^2, or 14% of the entire area. The actual floodable area is larger, since areas in southern Bolivia and high-altitude wetlands were not included in the JERS-based mapping, and floodplains in the southwestern Brazilian Amazon were not well delineated owing to the timing of the mosaics. In addition, floodplains of small but very numerous low-order streams, and small interfluvial wetlands, could not be mapped at the ~100 m resolution of the SAR mosaics. Analyses of Shuttle Radar Topographic Mission digital elevation data for the lowland Amazon indicates that these small streams reach up to 5 million kilometers in length (B. Forsberg, pers. commun.).

The distribution of wetlands throughout the basin is heterogeneous with some regional trends. About one-fourth of wetlands are in the Madeira basin. Nearly all the basins with less than 10% floodable area are in the eastern Amazon. The mainstem floodplain, which constitutes less than 2% of the total basin area, accounts for about 12% of the basin's wetlands. Basinwide, about three-fourths of wetlands are covered by forest, woodland, or shrubland. All large watersheds west of the Negro are at least 85% forested.

Chapter 4
Phytogeography, Species Diversity, Community Structure and Dynamics of Central Amazonian Floodplain Forests

Florian Wittmann, Jochen Schöngart, and Wolfgang J. Junk

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Abstract Amazonian floodplain forests are classified into nutrient-rich white-water floodplains (várzea) and nutrient-poor black-water and clear-water floodplains (igapó). Tree species distribution depends on sediment- and nutrient-loads of river waters, on flood regimes and hydro-geomorphic disturbance. The distribution of the different floodplain forest types is determined by adaptations of tree species to different levels and periods of flooding, and most habitats and species are strongly zoned along the flooding gradient. This leads to characteristic successional stages

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with distinct species composition, diversity, and forest structure. Amazonian floodplains and especially the várzea is covered by the most-species rich floodplain forest worldwide. Low flooded forests are floristically distinct from highly-flooded forests, and characterized by intense species exchange with the surrounding uplands. Highly-flooded forests are characterized by elevated degrees of endemic tree species. This indicates comparatively stable environmental conditions over large part of the Amazon basin since at least the early Palaeocene. It is likely that the Amazonian floodplains represented linear refuges for moist-sensitive tree species from the Amazonian uplands during periods with dryer climatic conditions.

4.1 Introduction

The high level of precipitation, its seasonality and the generally low slope inclinations in the Amazonian lowland lead to seasonally flooded areas along the main Amazonian river systems. Trees establishing in these floodplains make use of several different adaptations to cope with the periodic lack of oxygen in flooded soils and the associated reductions of the vegetation period. The high sedimentation rates next to white-water river channels, the scarcity of nutrients in the black-water and clear-water floodplains, and the anoxic conditions in the rhizosphere of backwater depressions accentuate the complex phyto-ecological interactions to which floodplain trees are exposed. Accordingly, the species richness of trees in Amazonian floodplains is lower than that in the surrounding terra firme (Prance 1979; Balslev et al. 1987). Recent studies, however, have shown that Amazonian floodplain forests are the most species-rich floodplain forests worldwide (Wittmann et al. 2006a). This can be explained by (a) the high diversity of habitats, whose establishment is dependent on water chemistry as well as on geohydrological (suspension load of the rivers) and biogeographical (e.g., forest succession, geographical diversity gradients, connectivity by means of the rivers) factors; and (b) the relatively stable environmental conditions within the Amazon basin over millions of years influenced, of course, by the changing spatial sizes and patterns of distributions of the areas. Even assuming tectonic and climatic changes during the Tertiary and Quaternary, it is likely that Amazonian floodplains existed over a long geological time span (Junk and Piedade 2010).

The first researchers to provide floristic and ecological descriptions of Amazonian floodplain forests were Huber (1910), Ducke and Black (1953), Takeuchi (1962), and Hueck (1966). Based on the hydrochemical differentiation of Amazonian floodplains in white-water, black-water, and clear-water influenced floodplains, as elaborated by Sioli (1954a,b), Prance (1979) emphasized the floristic differentiation of várzea forests (white-water) and igapó forests (black-water and clear-water). Várzea forests occur along the channels that drain the Andes and/or the Andean foothills, such as those of the Ucayali-Solimões-Amazon, Juruá, Japurá, Purús, and Madeira Rivers. These rivers are rich in suspension load, which is deposited along the river margins as well as in the channel bars, levees, lakes, and backwater depressions along the river courses. Due to the constantly annually persistent and partially extreme input of sediment, white-water rivers form highly dynamic systems of constantly migrating river channels, thus creating a variety of floodplain and forest microhabitats (Salo et al. 1986; Kalliola et al. 1991; Campbell et al. 1992). Várzea floodplains are exceptionally rich in nutrients, as reflected by the elevated net primary production (NPP) of their vegetation cover (Junk and Piedade 1993; Worbes 1997; Schöngart 2003; Schöngart and Queiroz 2010). These forests extend over an area of approximately 200,000 km^2 within the Amazon basin (Junk 1989).

Igapó forests occur along rivers that drain the Paleozoic and/or Precambric shields of Guyana (N) and Central Brazil (S), e.g., the Negro, Tapajós, and Xingú Rivers. These rivers carry low loads of suspended matter and solutes, resulting in a paucity of nutrients. Compared to the hydrogeomorphologic dynamic várzea, igapó forests form relatively stable floodplain habitats. Periodically flooded igapó floodplains cover an area of approximately 100,000 km^2 (Junk 1989). Detailed information on the geochemistry of várzea and igapó is given by Irion et al. (2010) and Furch and Junk (2010) and on wetland forest classification by Junk and Piedade (2010).

In contrast to non-flooded Amazonian forests, for which published databases report more than 250,000 trees in an inventoried area totalling more than 700 ha (Ter Steege et al. 2006), the number of inventoried trees in Amazonian floodplain forests is small. In várzea forests, floristic inventories have covered an area of less than 70 ha and approximately 40,000 voucher specimens (resumed in Wittmann et al. 2006a), whereas the databases for igapó forests contain inventories of less than 20 ha and approximately 11,000 trees (data from Rodrigues 1961; Keel and Prance 1979; Revilla 1981; Piedade 1985, Campbell et al. 1986; Ferreira 1991; Ayres 1993; Ferreira and Prance 1998; Haugaasen and Peres 2006; Inuma 2006). The overwhelming majority of studies on Amazonian floodplain forests have concentrated on várzea forests; consequently, much more knowledge is available concerning their botany, taxonomy, phytogeography, ecology, and tree physiology than is the case for igapó forests. This chapter summarizes our knowledge about the forest structure, tree species distribution along vertical and geographical gradients, and tree species diversity of Amazonian floodplain forests in relation to their abiotic environments. A classification of the different forest types is presented, and species oligarchies and endemisms within floodplain forests are discussed.

4.2 The Várzea Forest

4.2.1 Environmental Gradients and Successional Dynamics

Floodplain forests cover the transitional zone between aquatic and terrestrial habitats, which complicates interpretation of the environmental factors responsible for tree species composition and distribution (Breen et al. 1988). The average extent of flooding depends on the precipitation and discharge regimes as well as on the topography of the floodplains, and it varies along the river course. Thus, flooding can reach up to 16 m in western Amazonia, 10 m in central Amazonia, and 6 m in eastern Amazonia (Junk 1989; Lamotte 1990). The 'flood pulse' (Junk et al. 1989) is monomodal and therefore predictable, resulting in well-defined high-water (aquatic phase) and low-water (terrestrial phase) periods during the year.

Flooding superimposes and partially modifies other abiotic and biotic environmental factors that are of crucial importance for forest development (Junk et al. 1989). The periodic inundation of floodplain forests largely determines the species composition and distribution of their trees, because this process imposes a complex mixture of abiotic factors that interact with natural forest succession. On freshly deposited substrates along the main-river channels, new-site colonization by pioneer trees is an 'allogenic' induced succession (*sensu* Tansley 1929; Burrows 1990), in which species composition is triggered by the abiotic environment. During the following successional stages, habitats become more stable, particularly with respect to geomorphology, and abiotic factors may become relatively constant over decades, implying that allogenic succession is replaced by 'autogenic' succession (Wittmann et al. 2004).

Abiotic variables, such as flood height and duration, sedimentation rates, distance from the main-river channels, soil texture, and solar radiation on the forest floor, but also biotic variables, including species richness, stand density, stand architecture, mean wood density, and increment and growth rates of trees, are variables that change during forest succession and interact with each other. Thus, identification of one or two of these variables allows for reliable predictions about the others. Wittmann et al. (2002b) noted that forest succession in várzea forests is linked to the biogenically induced process of silting-up, so that it proceeds in relation to the increasing topographic level of the forested sites. This leads to the occurrence of distinctive várzea forest types, which differ in species composition and richness, stand age, and forest structure (see Fig. 4.3).

4.2.1.1 The Role of Flooding

Starting from considerations of the heights and durations of the periodic inundations and their impact on plant distributions in floodplains, Pires and Koury (1959) and Hueck (1966) described a zonation of plant communities along the flooding gradient in eastern and central Amazonian várzea. Junk (1989) investigated the distribution of tree species along the flooding gradient in várzea forests near Manaus. He reported different associations of tree species that establish at topographic levels with inundations lasting 140 (high-level tree community), 230 (low-level tree community), and 270 (low-lying shrub community) days year^{-1}. Ayres (1993) also observed the establishment of different várzea-forest types depending on the mean inundation height and length in várzea forests of the lower Japurá River. Applying the nomenclature used by the local population, he classified the forests as *chavascal* (mean inundation of 5.0–7.0 m), *restinga baixa* (2.5–5.0 m), and *restinga alta* (1.0–2.5 m).

Based on floristic inventories totaling an area of 5 ha in várzea forests at the lower Japurá River, near Tefé, and the lower Solimões River, at the confluence with the Negro River near the city of Manaus, Wittmann (2001) and Wittmann et al. (2002b) inventoried 2,631 várzea tree individuals (≥10 cm dbh) belonging to 306 species. Using high-resolution digital elevation models to the nearest 0.1 m together with data obtained from daily water-level records at the harbor of Manaus since 1903, the authors performed a one-dimensional ordination of all inventoried tree species in order to determine their occurrence along the flooding gradient. The results showed that the várzea tree species can be separated according to two main habitats: (a) *low-várzea forests*, influenced by mean inundations with heights between 3.0 and 7.5 m (corresponding to an mean inundation period of 50–230 days year^{-1}), and (b) *high-várzea forests*, influenced by mean inundations with heights of less than 3.0 m (mean <50 days year^{-1}). The terms *restinga baixa* and *restinga alta*, introduced by Ayres (1993), were used in that study in a modified form, because in Brazil *restinga* frequently refers to vegetation habitats in coastal areas, describing ecosystems with vegetation often adapted to edaphically or climatically induced aridity (Eiten 1970; Rizzini 1997; Wittmann et al. 2002a,b).

Of the tree species recorded by Wittmann (2001) and Wittmann et al. (2002b), only 54 (17.5%) occurred in both low várzea and high várzea, demonstrating the striking difference between the two habitats. The majority of the inventoried tree species (50.2%) were concentrated in the high várzea, with 32.3% restricted to the low várzea. Variations in tree species richness were highest between sites subjected to mean inundations between 3.0 and 2.5 m, thus justifying the habitat differentiation between low várzea and high várzea at these elevations (Fig. 4.1).

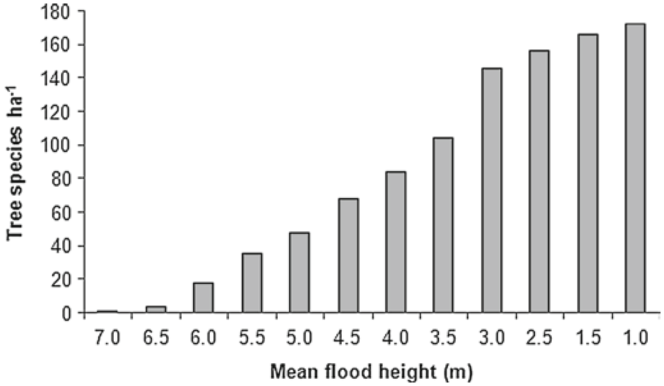

Fig. 4.1 Tree species richness ≥10 cm dbh along the flooding gradient. Highest variations in species richness occur between forest plots with mean flood heights of 3.5–3.0 m. Data are from forest inventories of the Mamirauá Sustainable Development Reserve, near Tefé, and at the lower Solimões River, near Manaus (Wittmann 2001), where 83 plots of 625 m^2 were nested along the mean inundation height (daily water-level records in the harbor of Manaus from 1903 to 2003) of 2,631 individual trees

The continuous increase in species richness with decreasing inundation height and length, and the pronounced species zonation of trees in várzea forests along the flooding gradient were later investigated on a continental-wide scale. Wittmann et al. (2006a) made use of data from 44 floristic inventories totaling an inventoried area of 62.34 ha scattered over ten regions along the Amazonian várzea river system, including sites in Brazil, Peru, Bolivia, Colombia, and Ecuador. These authors found that mean species richness in low-várzea forests averaged 56.9 species ha^{-1}, with 100.8 species ha^{-1} in high-várzea forests (≥10 cm dbh).

The pronounced zonation of várzea tree species along the food-level gradient leads to characteristic species associations and forest types. Only a few tree species occur along the entire flooding gradient; instead, most of them are restricted to very small topographic amplitudes (Wittmann 2001; Parolin et al. 2002c; Wittmann et al. 2002b). Section 2.1.3 provides an overview of várzea-forest types and cites the most characteristic tree species.

4.2.1.2 Geomorphologic Site Dynamics and Habitat Stability

Besides flooding, the processes of sedimentation and erosion and the physical features of the substrate are determining environmental factors in the development of different várzea-forest types (Salo et al. 1986; Terborgh and Petren 1991). Species composition in floodplains varies widely, depending on the frequency of river disturbances (Oliveira-Filho et al. 1994). The periodic deposition and removal of litter and thus of seed banks affect seed and seedling recruitment, and therefore the selection of species able to survive in these areas (Metzger et al. 1997). Next to the main-river channels, sedimentation on slip-off slopes can reach 0.3–1 m year^{-1} (Junk 1989; Campbell et al. 1992) (Fig. 4.17b). On undercut slopes, erosion can wash out several hectares of forests during a single high-water period (Wittmann 2001, Fig. 4.17c). The unstable habitat conditions caused by sedimentation and erosion result in a highly diverse patchwork of microhabitats (Kalliola et al. 1991; Campbell et al. 1992), which is reflected by the floristic and physiognomic structure of the forest cover (Fig. 4.17a).

In general, sedimentation and soil texture are linked to both the distance of the sites from the main-river channels and the period of inundation to which the sites are subjected (Mertes et al. 1995; Wittmann et al. 2004). Moreover, there exist strong linear correlations between these variables (Fig. 4.2). Water current is highest next to the main-river channels, where sedimentation rates are high and relative coarse fractions, such as sand, are deposited at the banks of islands and river margins. With increasing distance from the rivers, current energy is reduced by the water resistance posed by levees and the vegetation cover, resulting in low sedimentation rates. Consequently, mostly fine grained matter, such as silt and clay, is deposited, especially when the floodwaters are non-turbulent and persist for several weeks or months in oxbows, lakes, and backwater depressions. Due to reduced flood duration and current energy, the substrate of high-várzea forests in general has a finer texture than that of low-várzea forests near the main-river channels.

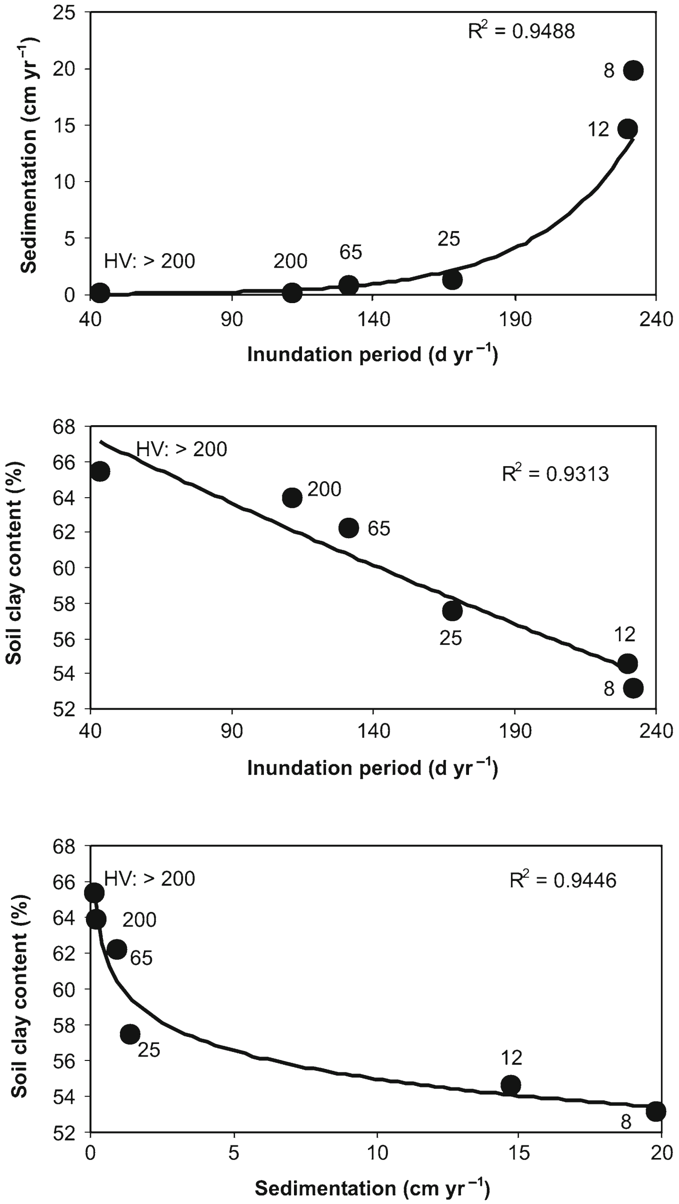

Fig. 4.2 Mean inundation period plotted against annual sedimentation rates (**a**) and the soil clay content (**b**) in forest plots (each 1 ha) with mean stand ages of 8, 12, 25, 65, 200, and >200 years (HV = high várzea); annual sedimentation rate plotted against soil clay content (**c**). Data originate from Wittmann (2001), Schöngart (2003), and Wittmann et al. (2004)

The small-scale changes of sedimentation rates and substrate texture directly influence the distribution of tree species (Wittmann et al. 2004). On the one hand, drainage in coarse-grained soils is better than in fine-grained soils, where oxygen is rapidly consumed due to the decomposition of accumulated organic matter by microorganisms (Larcher 1994). On the other hand, sites with coarse-grained substrates undergo high sedimentation rates, which impede seed germination and seedling establishment, and which cover surface roots and thus affect aeration for mature individuals. Only a few tree species, including *Salix martiana* Leyb. and *Alchornea castaneifolia* (Humb. & Bonpl. ex Willd.) A. Juss. in central Amazonian and *Tessaria integrifolia* Ruiz & Pav. in western Amazonian várzea, are sufficiently adapted to establish at these sites (Lamotte 1990; Worbes et al. 1992). These species avoid anoxia at the root level by forming new-root layers above the annual deposits (Wittmann and Parolin 2005). They also develop deep reaching primary roots, which improve stability against water turbulence during high-water periods and also may facilitate water uptake from river and ground waters during terrestrial phases.

Off the main-river channels, topographic depressions in the form of oxbows and lakes are characterized by slow-current floods. As a consequence of the typically concentric shapes of depressions and levees, floodwaters reach these sites from downstream, against the vector of river currents (Irion 1984b). Sediments deposited in these depressions thus lack coarse grains and drain poorly. Due to the long-term inundation, organic material accumulates. Anoxia at the root level may persist throughout the year. The type of forest that becomes established in these depressions is known as *chavascal* (in Brazil, Ayres 1993) and *bajeal* (in Peru, Lamotte 1990). In addition, a specific form of swamp forest can develop on floating islands of organic material and is locally called *matupá* (Junk 1983; Junk and Piedade 1997).

4.2.1.3 Forest Succession and the Várzea Forest Types

Worbes et al. (1992) defined the várzea-forest types of the lower Solimões River near Manaus by the abundance and dominance of characteristic tree species, and the age structure of forest stands as determined through dendrochronological methods. After the establishment of grasses on freshly deposited alluvial sediments, the first-colonizing pioneer trees form monospecific stands, but these are swiftly replaced by tree species of early-secondary stages. Late-secondary species are, in turn, replaced by intrusion of late-successional or ‘climax’ species. The successional sequence (sere *sensu* Ricklefs 1990) results in a continuous increase in species diversity but a decrease in stand densities. The sere is, moreover, characterized by a reduction of the mean diameter increments and an increase in mean wood-density, as a consequence of the higher abundance of slow-growing, long-living shade-tolerant species in late-successional forests (Lamprecht 1986; Worbes 1997; Schöngart et al. 2003).

The classification of várzea forests by Worbes et al. (1992) along the successional sequence is valid for most low-várzea forests of central Amazonia. Forest succession proceeds in a well-established sere and in interaction with changing environmental conditions. However, the successional model does not take into account three other várzea-forest types, which are scarce in the region near Manaus but very frequent in the western Amazonian várzea: (1) high-várzea forests, (2) primary successions along lakes, and (3) chavascal. These forest types are present when the strength of habitat dynamics is reduced.

Based on the floristic inventories of Wittmann (2001) and Schöngart (2003), who accumulated data from 10 ha in the Mamirauá Sustainable Development Reserve (confluence between the Solimões and the Japurá Rivers) and near the city of Manaus (lower Solimões River), different types of várzea forests can be distinguished. These are characterized by typical patterns of tree species occurrence, dominance, diversity, and by forest structure. In the following, the most important types of várzea forest are presented. The nomenclature used is that of Worbes et al. (1992) and Ayres (1993), but in the modified and completed form suggested by Wittmann et al. (2002a,b, 2004) and Schöngart (2003) and discussed in Junk and Piedade (2010).

In undisturbed equatorial terra firme forests the regeneration cycle commonly starts in small to medium (<1 ha) sized gaps caused by mortality of single trees, or collapse of groups of trees in the top canopy. In contrast the regeneration cylce in the várzea is driven by the forces of erosion and deposition, which continuously create large areas for new-site colonization (Fig. 4.18f, g). Basically, two types of primary successions in várzea forests can be distinguished. These depend on the hydrogeomorphologic site conditions and the period of plant community development (Fig. 4.3). Both types eventually result in late-secondary forests.

Primary Succession Type One: Pioneer Forests Along Rivers and River Channels On freshly deposited sediments, the first colonizing tree species of the pioneer forest at flood-levels below 7.5 m (corresponding to mean flooding periods of 230 days year^{-1}) are *Alchornea castaneifolia* and *Salix martiana*. These species possess adaptations against high and prolonged inundations and against high sedimentation rates, but they only establish at sites where relative photosynthetic active radiation (rPAR) amounts to 70–100% (Wittmann and Junk 2003). As light-demanding pioneer species, they are characterized by fast growth, relatively short life cycles, and a high potential for vegetative and sexual reproduction (Puhakka and Kalliola 1993; Worbes 1997). The buoyant seeds of *S. martiana* germinate while the seeds float on the water surface, thus enhancing plant establishment as soon the seedlings land on a substrate, which marks the beginning of the terrestrial phase (Oliveira Wittmann et al. 2007a). Pioneer forests generally form stands with uniform and single-storied and open canopies (Wittmann et al. 2004). Mean maximum tree ages are only 10 years (Worbes et al. 1992). At the central Amazon várzea, *A. castaneifolia* is generally more abundant in pioneer forests than *S. martiana*. The latter seems to undergo cyclic reproduction and establishment periods, disappearing locally from stands for periods of several years (Oliveira 1998).

The establishment of the pioneer forest promotes sedimentation because the stems and roots of the trees reduce water current energy, thus leading to a continuous up-lifting of the topographic levels of the stands (Wittmann et al. 2002a,b, 2004).

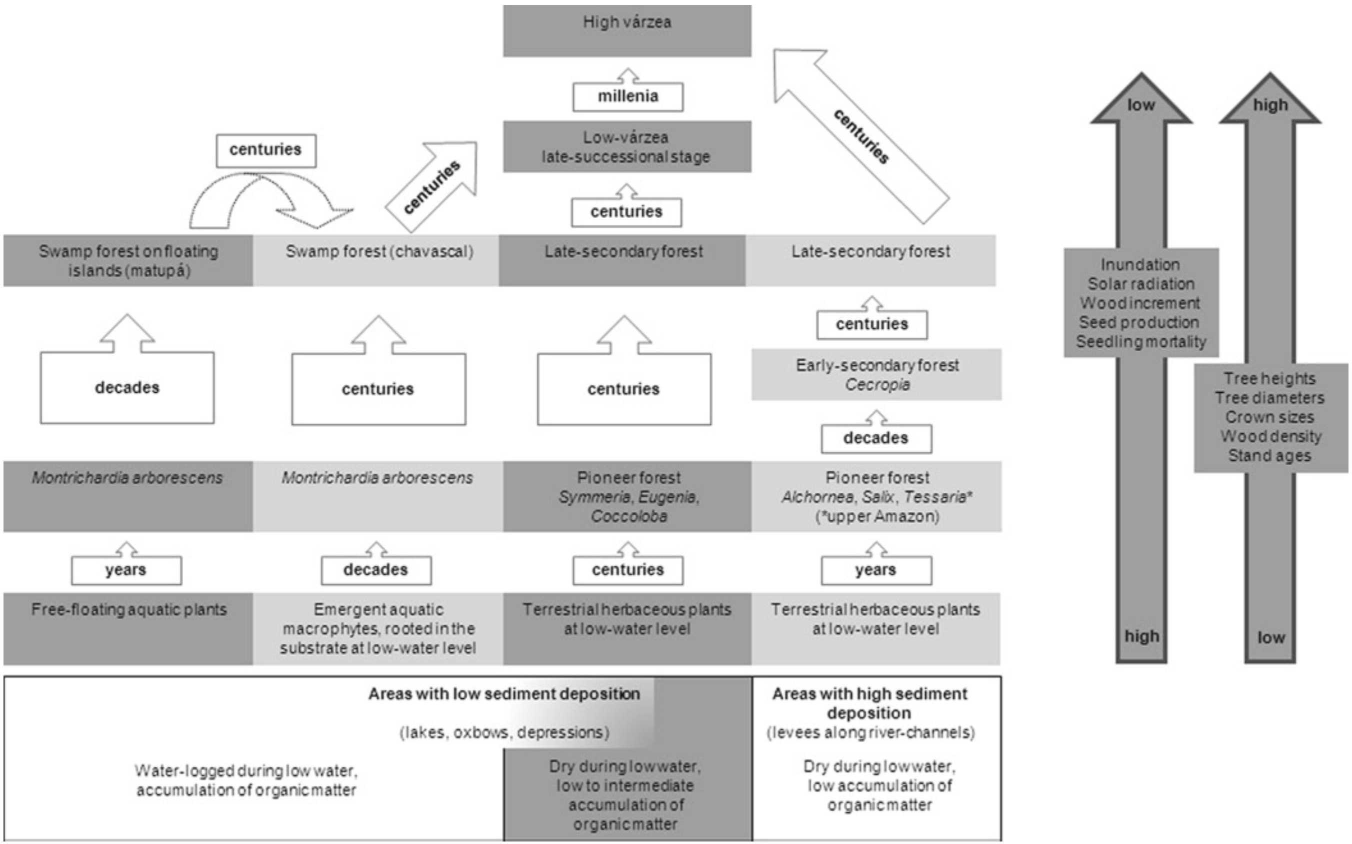

Fig. 4.3 Schematic types of forest succession in várzea floodplains. Note that the term "secondary forest" not refers to antropogenic disturbance, but to natural stages of forest succession according to Budowski (1965) and Worbes et al. (1992)

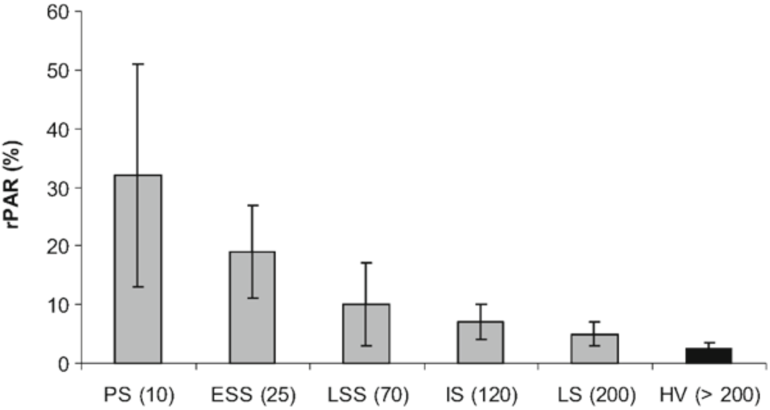

Fig. 4.4 Mean rPAR (relative photosynthetic active radiation) at the forest floor in six different successional stages (with mean stand age in years). Data are from repeated measurements taken from at least seven aleatoric points within 1-ha forest plots (Wittmann 2001; Schöngart 2003; Wittmann and Junk 2003). PS, pioneer stage; ESS, early-secondary stage; LSS, late-secondary stage; IS, intermediate stage; LS, late successional stage of the low várzea; HV, late successional stage of the high várzea

Moreover, the species comprising these forests shade their environment, reducing the establishment of grasses and promoting the growth of other, moderately light-demanding tree species ('inhibition' and 'facilitation' *sensu* Connell and Slatyer 1977). After the establishment of early-secondary tree species, pioneer species no longer regenerate because the light conditions necessary for successful establishment are no longer present. The rPAR below the canopy of early-secondary species decreases already to about 32% ± 19% (Wittmann 2001; Fig. 4.4). The initial establishment of *Salix* and *Alchornea* is severely hindered by the perennial, highly productive C_4 grasses *Paspalum fasciculatum* Willd. ex Flügge and *Echinochloa polystachya* (Kunth) Hitchc., which compete with these trees for light (Piedade et al. 1991, Fig. 4.18i).

Primary Succession Type Two: Pioneer Forests in Floodplain Lakes Sediment input in floodplain lakes is low and the grain size of the sediments is fine. The substrate of the bottom of the lakes is composed of poorly aerated clays. Lake margins that are exposed to annual inundations of less than about 270 days year^{-1} are colonized by highly flood-resistant shrubs (*Symmeria paniculata* Benth., *Eugenia* spp., *Cocoloba* spp.); either isolated or forming dense stands (Fig. 4.18j). In contrast to the chavascal, which establishes in topographic depressions, organic material near the lake margins is removed by wind-induced currents. In the inner part of dense stands of *Symmeria paniculata*, a litter layer may accumulate, because the stands fall regularly dry. *Salix* and *Alchornea* do not occur, probably because of the poor aeration of the clay soils. *S. paniculata* stands may be stable for many decades because of the low sediment input (Fig. 4.3). These shrubby species often rejuvenate and propagate vegetatively, and seedling establishment occurs only in multi-annual periods of extremely low water levels (Junk 1989). Allogenic succession with species of late-secondary forests proceeds only when the length of the flood period decreases as a result of the build-up of the rise of the lake bottom.

Early-Secondary Stage Along Rivers and River Channels These stages are dense and often monospecific non-stratified, mono-layered stands of *Cecropia latiloba* Miq. (Worbes et al. 1992) (Fig. 4.18i), with up to 1,000 individuals ha^{-1} (≥10 cm dbh; Schöngart 2003). Mean maximum tree ages are 15–20 years (Worbes et al. 1992; Schöngart 2003). These forests often can be found near main-river channels. Their canopy height is related to the age of the deposited sediment and the sequence of establishment. In central Amazonia, early-secondary stages occur on sites where the mean inundation height ranges from 6.0 to 4.5 m. With their dense stands, these forests also favour the biogenic silting-up of their sites, by reducing the impact of flooding and stabilizing the substrate. Combined with the reduced solar radiation below their canopies (Fig. 4.4), early-secondary forests facilitate the establishment of late-secondary tree species.

Late-Secondary Stages Late-secondary stages near river shores are composed of about 500–600 individuals, belonging to 20–50 tree species ha^{-1} (Wittmann et al. 2004) (Fig. 4.17d). This stage is characterized by a beginning stratification. Characteristic species in the upper canopy are *Pseudobombax munguba* (Mart. & Zucc.) Dugand, *Laetia corymbulosa* Spruce ex Benth., and *Luehea cymulosa* Spruce ex Benth., while those in the lower canopy are *Maclura tinctoria* (L.) D.Don ex Steud., *Nectandra amazonum* Nees, and *Crateva benthamii* Eichler. The inundation height is generally between 5.0 and 4.0 m, with the inundation period lasting 210–160 days year^{-1}. Mean maximum stand ages are 60–80 years (Worbes et al. 1992). The rPAR reaching the forest floor averages 10% ± 7% (Fig. 4.4). In lake basins, tree densities and species richness are often lower because of long flood periods.

Late-Successional Stage Low-Várzea Forests Late-successional stage forests of the low várzea contain 70–90 species ha^{-1}. The inundation height is between 4.5 and 3.0 m, corresponding to an inundation period of 50–120 days year^{-1}. These forests are well-stratified, but the sub-canopy stratum is characteristically poor in individuals (Fig. 4.17e). About 40% of all trees (≥10 cm dbh) belong to the upper canopy at a height of 30–35 m. Characteristic species in the upper canopy are *Piranhea trifoliata* Baill., *Tabebuia barbata* (E. Mey) Sandwith, and *Hevea* spp., in the lower canopy *Pouteria* spp., *Oxandra* spp., and *Duroia duckei* Huber. The rPAR at the forest floor in low-várzea late-successional stages averages 3–5% (Fig. 4.4). Maximum stand ages of approximately 400 years were recorded in *Piranhea trifoliata* (Worbes et al. 1992). According to Worbes' model of forest succession, the elevated ages of the trees suggest that late-successional forests of the low várzea are the mature 'climax' stage of the successional sere. This is certainly true in areas distant from river channels, where sedimentation rates are very low (<1 mm year^{-1}). The floristic inventories of Cattanio et al. (2002) in eastern Amazonia, Wittmann et al. (2002b) in central Amazonia, and Balslev et al. (1987), Dallmeier et al. (1996), and Nebel et al. (2001d) in western Amazonia, however, suggest that low-várzea late-successional forests are vulnerable to the changing environmental site conditions, and are eventually replaced by forests of the high várzea. Depending on the sedimentation rates in late-successional low-várzea forests, this development may require several centuries to millennia and thus allows for the establishment of several intermediate late-succession forest types.

High-Várzea Forest These are the most species-rich of the various types of várzea forests. In the central and western parts of Amazonia, tree species richness may be as high as 120–160 species ha^{-1} (Balslev et al. 1987; Dallmeier et al. 1996; Nebel et al. 2001; Wittmann et al. 2002b). High-várzea forests establish above a mean flood level of 3.0 m. Depending on the position along the flood-level gradient, the mean inundation period in high-várzea forests barely reaches more than 50 days year^{-1} and may fail completely during exceptionally dry years (e.g., during El Niño events; Schöngart et al. 2004). Many tree species occur with low abundances, often being represented by only one individual ha^{-1}. These forests show a distinctive stratification, with an upper canopy height at 30–35 m and emergent trees reaching heights of up to 45 m. Due to the relatively long terrestrial phases, trees regenerate during most of the year, thus leading to a characteristically dense under-storey (Fig. 4.18l). In central Amazonia, abundant genera in the upper canopy include *Terminalia, Aspidosperma*, and *Guarea*; in the mid-canopy, *Pouteria*, *Brosimum*, and *Eschweilera*; and in the low canopy, *Inga*, *Duguetia*, and *Annona*.

High-várzea forests can be classified as the climax of the várzea's successional sequence (Wittmann et al. 2002a,b). They often establish along the elevations along the banks of rivers and secondary-river channels (Fig. 4.18k). Due to the relatively long period of their geomorphologic development, which increases the probability of habitat fragmentation through the constantly moving beds of rivers and river channels, high-várzea forests occur on approximately 10–15% of the várzea's forested landscape (Wittmann et al. 2002a,b). The overwhelming fraction of its substrate is clayish (Fig. 4.2). The rPAR at the forest floor averages only 1–3%, which is similar to the light conditions found in undisturbed terra firme forests (Wittmann and Junk 2003; Fig. 4.4).

Chavascal The term *chavascal* (Ayres 1993) was first used during the nineteenth century in the *Flora Brasiliensis* (Martius 1840–1906) to describe species-poor and dense gallery forests in the Caatinga of southern Mato Grosso. In the central Amazonian várzea, the chavascal is a dense and species-poor forest that establishes in depressions and oxbows. The trees often develop stilt roots and aerial roots as outgrowths on their stems to improve aeration by increased root superficies (Wittmann and Parolin 2005). The chavascal cannot be included in the successional sequence that occurs next to the main-river channels, because succession follows a non-cyclic sere (*sensu* Schroeder 1998) in which changes in environmental conditions occur more slowly than near the highly dynamic river banks (Fig. 4.3). As an alluvial relict developing in old river oxbows or lakes, the chavascal is characterized by the slow silting-up of clayish deposits and organic matter in still waters (Wittmann et al. 2004). The input of fine-grained deposits during aquatic phases leads to an impermeable substrate, known as *tabatinga* to the Brazilian floodplain inhabitants. The poor drainage induces waterlogging of the vegetation cover even during low-water periods. Sedimentation rates measured in a chavascal at the lower Japurá River were 0.1–0.2 cm year^{-1}, and the soil clay content exceeded 80% (Wittmann et al. 2004).

The longstanding stable geomorphologic conditions combined with the anoxia at the root level during most of the year leads to a successional sequence in which primary stages reach ages of several decades. Characteristic species of primary successional stages within the chavascal are, especially, Polygonaceae of the genus *Symmeria*, and Myrtaceae of the genus *Calyptranthes* and *Eugenia*. These mostly arbustive trees form monospecific and highly dense stands (Wittmann and Parolin 2005). They establish at the banks of depressions, tolerating inundation heights of 7.0–7.5 m (up to 230 days year^{-1}). Year-ring counting on stem-discs obtained within the Mamirauá Reserve from *Calyptranhtes multiflora* Poepp. ex O. Berg and *Eugenia ochrophloea* Diels indicate maximum tree ages of 40–60 years (J. Schöngart and F. Wittmann, 2005, unpublished data).

The pioneer stages of the chavascal migrate towards the center of depressions, as silting-up proceeds and new sites become available for tree colonization. When inundation is reduced to <7.5 m high (<230 days year^{-1}), pioneer species of the chavascal are replaced by palms (mainly *Bactris* spp.) and a few dicots, such as *Buchenavia oxyxarpa* and *Pseudobombax munguba*. The mineral soil-surface of the chavascal is often undulated because tree fall leads to the formation of small elevations and depressions that become filled with water, also during the low-water period, and accumulate organic debris. In a floristic inventory of 625 m^2 within the Mamirauá Reserve, Wittmann et al. (2004) recorded eight tree species (≥10 cm dbh) in a chavascal inundated by a mean water column of 6.8 m. Stand density in this forest exceeded 600 individuals ha^{-1}; the non-stratified canopy was recorded at heights between 12 and 18 m.

Matupá A specific type of swamp forest develops on floating islands of organic material, locally called *matupá* (Fig. 4.3). These islands can develop in small lakes that do not fall dry. Floating aquatic plants build an organic layer that becomes colonized by moisture-tolerant sedges, ferns, and other herbaceous plants. When the tree-like *Montrichardia arborescens* (L.) Schott (Araceae) invades this layer, it stabilizes the organic material with its strong stolons and allows colonization by trees such as *Cecropia latiloba*, *Vismia* spp., and *Pseudobombax munguba*. The floating layer follows the water-level fluctuations of the lake. Permanent waterlogging reduces decomposition of the organic material, whereas extreme floods and droughts can destroy these islands (Junk 1983; Junk and Piedade 1997).

4.2.1.4 Forest Structure

In várzea forests, the successional sere is characterized by a typical distribution of tree densities, tree heights, tree diameters, crown sizes, and crown area coverage (Klinge et al. 1996; Worbes 1997; Wittmann et al. 2002b; Schöngart 2003).

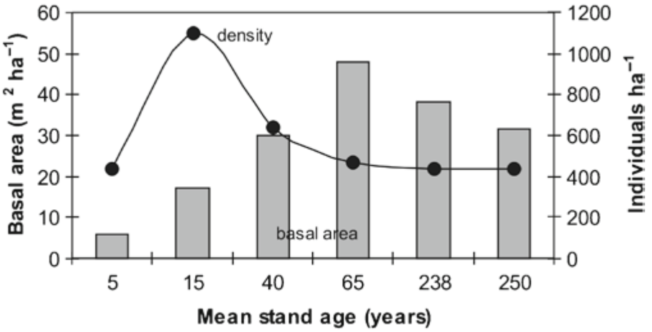

Fig. 4.5 Stand density and basal area of forest stands (trees ≥10 cm dbh) plotted against mean stand age (Data from Wittmann 2001; Schöngart 2003)

In pioneer stages along rivers and channels, tree densities ≥10 cm dbh average 400–500 individuals ha^{-1}, with the highest values occurring in early-secondary stages (800–1,000 individuals ha^{-1}). In subsequent successional stages, tree densities decline continuously to the average level (Fig. 4.5). The basal area of trees ≥10 cm dbh increases from the pioneer stages until the forests reach stand ages of 60–100 years. In later successional stages, the basal area declines (Fig. 4.5). The basal area of tree regeneration, however, shows an opposite trend: it tends to increase continuously from pioneer stages to old-growth forests (Wittmann and Junk 2003).

Mean and maximum tree heights, sizes of individual tree crowns, and the crown area coverage of várzea forests show a strong logarithmic relationship to the mean stand age of forests along the successional sere (Fig. 4.6, Wittmann et al. 2002b; Schöngart 2003). Pioneer stages and early-secondary stages are characterized by a non-stratified canopy establishing at heights of 8–12 m and 15–20 m, respectively. Late-secondary forests show a beginning stratification, with an upper canopy at heights of 20–25 m and a lower canopy at 10–15 m. Low-várzea late-successional forests are well-stratified: the upper canopy is established at 30–35 m, the mid-canopy stratum at 15–20 m, and the low-canopy at 5–10 m (Wittmann et al. 2002b). This stratification pattern is also valid in high-várzea forests, but here emergent trees of up to 45 m are found. By contrast, the chavascal is characterized by a single-layered canopy at heights of 12–18 m (Wittmann et al. 2004).

The different forest-structure patterns in the várzea allow for a reliable classification of várzea-forest types by remote-sensing techniques (Wittmann et al. 2002a,b). The non-stratified, homogeneous, upper-canopy surfaces of young successional stages and the chavascal are due to dense stands, generally small tree crowns, and high crown area coverage, which in turn result in homogeneous light reflectance patterns, as seen in aerial photographs and optically based satellite image data, such as SPOT HRV and Landsat TM (Fig. 4.7). In contrast, the more complex architecture of late-successional stages and, in particular, high-várzea forests can be

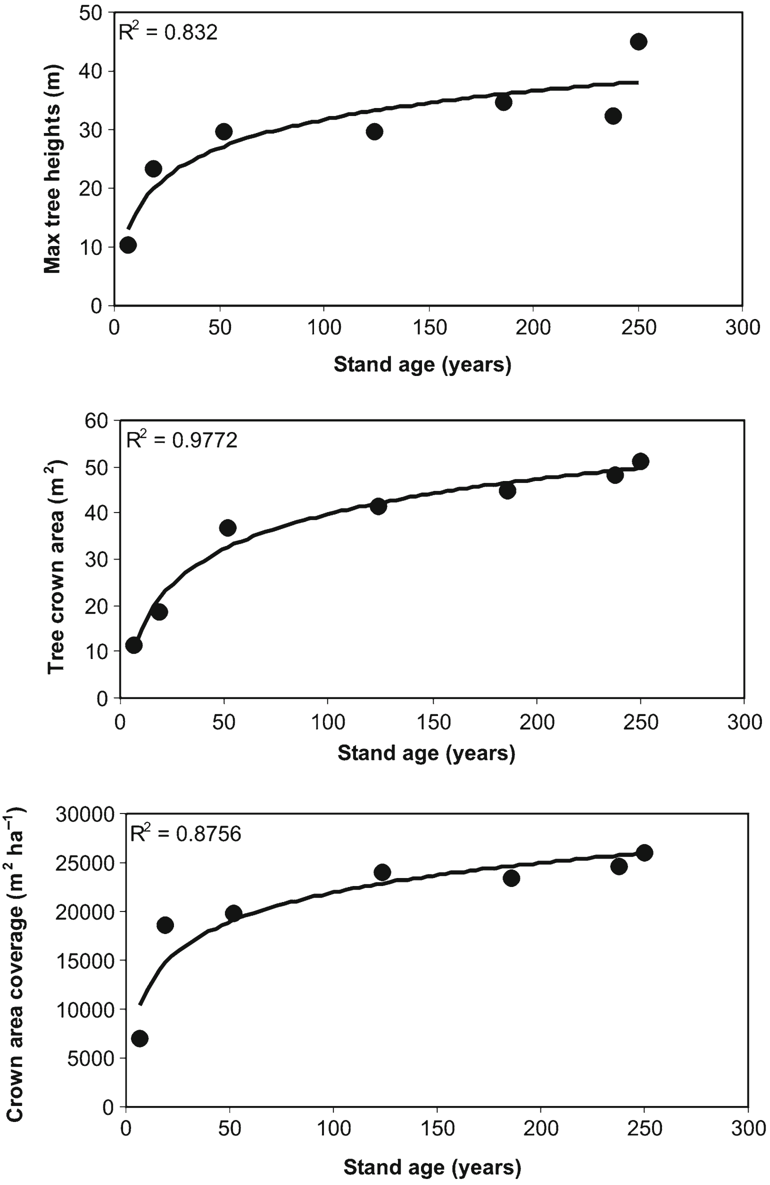

Fig. 4.6 Mean stand age of seven 1-ha forest plots plotted against mean tree heights of upper-canopy trees (**a**), mean crown area of upper-canopy trees (**b**), and mean crown area coverage of understorey and upper-canopy trees (ha^{-1}) (**c**). Data originate from Wittmann (2001) and Schöngart (2003)

traced back to the stratified canopies, different crown sizes, and lower crown area coverage resulting from the natural mortality of trees with partially extensive crowns. Consequently, the light reflectance patterns of the upper-canopy surfaces of these forests are more diffuse (Fig. 4.7; Wittmann et al. 2002a,b).

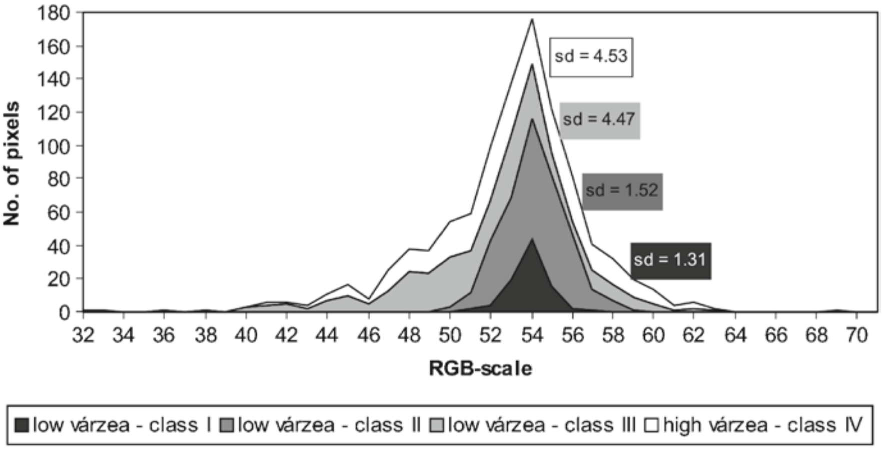

Fig. 4.7 Light reflectance patterns (RGB scale) of different várzea forest types scanned by LANDSAT TM image data. Low-várzea class I = early successional stage, low-várzea class II = early secondary stage, low-várzea class III = late-successional stage, high-várzea class IV = climax stage (Data modified from Wittmann et al. 2002b)

4.2.1.5 Population Structure and Regeneration Behaviour

The successional sequence is accompanied by different strategies regarding the dispersal, establishment, and growth of tree species. Wittmann (2001) investigated the spatial distribution of várzea species and associations along gradients of flooding, substrate texture, and incoming solar radiation on the forest floor. The author concluded that tree regeneration (<10 cm dbh) of many species show greater amplitudes of spatial distribution along these gradients than the mature tree population (≥10 cm dbh). The 96 mature individuals of *Pseudobombax munguba*, part of an inventory totaling 5 ha, for example, concentrated on an elevation with a mean inundation height of 4.63 ± 0.6 m, whereas the 158 individuals of tree regeneration in 40 aleatoric plots totaling 3,125 m^2 and located at the same sites concentrated on elevations where the mean inundation was 5.43 ± 1.8 m. This variation in species distribution patterns suggests that the mortality of already established seedlings or saplings of *P. munguba* is high, and that individuals are no longer competitive when establishing outside the optimal range of environmental conditions. In fact, the majority of the várzea's tree species are restricted to very small ecological amplitudes and habitats. Moreover, succession implies that for most várzea species the optimal range of conditions are present only during a restricted period within the successional sere. In early-successional stages, many of the trees do not successfully compete when regenerating at the same site as the parent trees.

Wittmann and Junk (2003) and Oliveira Wittmann et al. (2007b) investigated the structure and species composition of tree saplings (1–10 cm dbh) and tree seedlings (≤1 cm diameter; ≤1 m height) compared to the mature tree population (≥10 cm dbh)

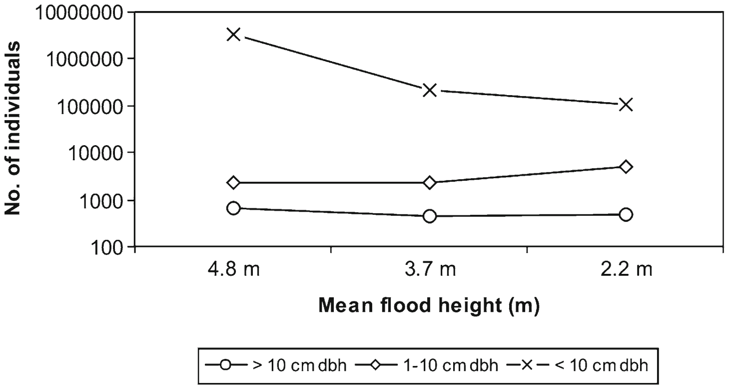

Fig. 4.8 Individual densities of várzea trees ≥10 cm dbh and tree regeneration (saplings = 1–10 cm dbh; seedlings = <1 cm dbh and <1 m height) in three várzea successional stages at different flood heights

in three várzea-forest types of different ages and inundation heights. The density of mature trees declined from 641 individuals ha^{-1} in a secondary forest (40 years, 4.8 m) to 434 individuals ha^{-1} in a late-successional forest (180 years, 3.7 m), and increased slightly, to 469 individuals ha^{-1}, in a high-várzea forest (>200 years, 2.2 m). By contrast, the density of saplings increased from 2,256 to 2,336 and 5,056 individuals ha^{-1}, respectively. The seedling density decreased from more than 3,000,000 individuals ha^{-1} in the secondary forest to about 210,000 individuals ha^{-1} in the late-successional plot and to about 110,000 individuals ha^{-1} in the high-várzea forest (Fig. 4.8). The majority of tree species in the secondary forest were represented by individuals at all community levels, i.e., the seedling, the saplings, and the mature tree community. This indicated that regeneration in these overall-dispersing species occurs frequently, despite the high impact of flooding. However, mortality rates in these species are high: the ratio seedlings-saplings-mature trees in this early stage of succession was 100–0.07–0.02. Thus, seedling mortality rates of at least 99.98% can be expected (in fact, they must be higher because both of the inventories mentioned above took place during a few weeks of the terrestrial phase, but many more seedlings may establish and die during a single vegetation period). The proceeding forest succession and decreasing impact of flooding lead to an increased number of tree species with low but more efficient reproduction strategies. Seedling densities in late-successional forests are low, but so are mortality rates. The ratio seedlings-saplings-mature trees were 100–1.1–0.2 in the late-successional low-várzea forest and 100–4.6–0.4 in the high-várzea forest (Oliveira Wittmann et al. 2007b).

The population structure of most of the várzea trees is a reverse-J-shaped curve (Fig. 4.9), which is characteristic for natural forests and well-known to be typical for many tropical forest types (Budowski 1965; Bazzaz and Pickett 1980; Denslow 1980; Whitmore 1989; Hubbell and Foster 1992). While most early-secondary

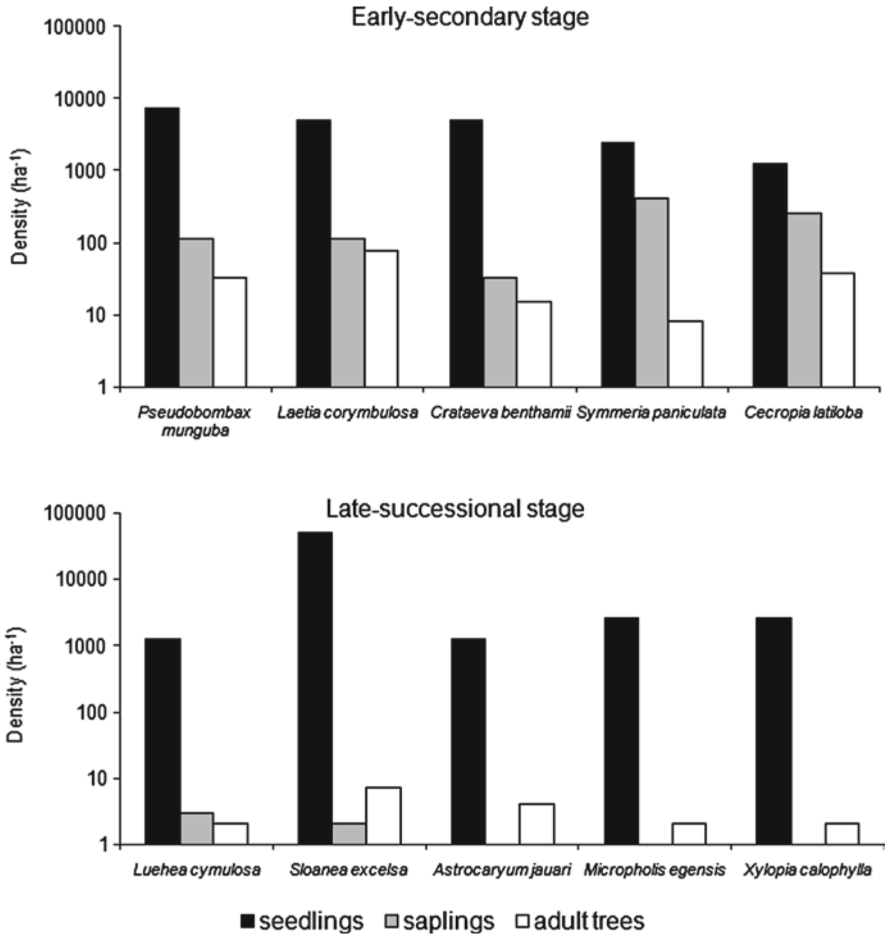

Fig. 4.9 Population structure of several várzea tree species in an early-secondary (**a**) and a late-successional (**b**) stage. Seedlings = <1 cm dbh and <1 m height; saplings = 1–10 cm dbh; mature trees = ≥10 cm dbh

species are represented in all community levels, seedling, sapling, and the mature tree community, most late-secondary and late-successional species lack individuals at the sapling level (Fig. 4.9). This indicates that many individuals of these species are eliminated after establishment and therefore may need exceptional environmental conditions to establish successfully, such as consecutive years with low inundations in less flood-tolerant species, or the creation of a gap by tree fall in light-demanding species or *opportunists* (*sensu* Bazzaz 1991).

Tree regeneration in várzea forests thus primarily depends on the flood pulse, but it is also linked to incoming solar radiation on the forest floor (Wittmann and Junk 2003). Early-successional tree regeneration is composed of light-requiring

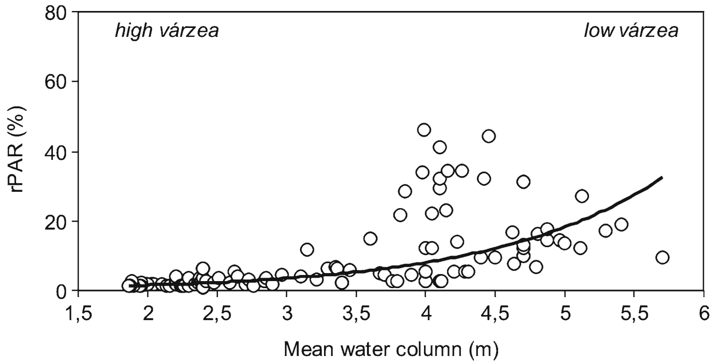

Fig. 4.10 Mean spatial distribution center (MDC, Ebdon 1998) of sapling species (1–10 cm dbh) along flooding and irradiation gradients on the forest floor in a várzea inventory of 24 plots totaling 1,875 m^2 (Wittmann and Junk 2003)

species, whereas the number of ecological niches with respect to radiation variability is low. Together with the decreasing impact of flooding, the more complex forest architecture in late-successional forests implies a high number of ecological niches at the seedling and sapling levels. Species richness and the density of saplings increase, resulting in shade-tolerant species groups that establish under closed forest canopies, and in light-tolerant species groups that establish near the forest borders and in gaps (Fig. 4.10). In the high várzea, the height and duration of flooding are reduced to the extent that regeneration during most of the year is terrestrial, and thus similar to that of non-flooded environments. However, the flood pulse in high-várzea forests probably remains a limiting factor influencing species composition with respect to tree regeneration. Kubitzki (1989a) stated that the origin of many várzea trees is the surrounding terra firme. When those trees immigrated to the floodplains, they gradually developed adaptations to the periodic inundations. For this reason, many high-várzea species have probably developed less pronounced adaptations to flooding than low-várzea species (Wittmann et al. 2002b) and may react very sensitively even to small flood-pulse variations.

4.2.2 Tree Species Composition and Diversity Gradients

Compared with the surrounding terra firme and despite the fact that fewer inventories and smaller databases are available, Amazonian floodplain forests are taxonomically relatively well-described. Of about 1,000 flood-tolerant tree species occurring in the white-water floodplains across the Amazon basin (Wittmann et al. 2006), 450 were already described during the first half of the nineteenth century by only eight botanists (with decreasing numbers of species descriptions: Bentham, Martius, Aublét, De Candolle, Spruce, Poeppig, Linné, and Willdenow). This emphasizes the easy accessibility of floodplain forests by these researchers; but it also demonstrates that

Amazonian várzea forests are a special ecosystem with a restricted number of tree species that are partially widely distributed.

4.2.2.1 Floristic Patterns at the Family Level

Representatives of nearly all plant families characterizing the neotropical flora of woody plants can be found within the floodplain forests – to some extent with the same relative importance as in the terra firme (Maas and Vestra 1993). Based on data from large-scale floristic inventories in terra firme forests, i.e., those described by Gentry (1992), Terborgh and Andresen (1998), Ter Steege et al. (2000, 2006), and Pitman et al. (2001), the most important tree families in neotropical terra firme forests are (with decreasing importance): Fabaceae, Moraceae, Annonaceae, Euphorbiaceae, Lauraceae, Sapotaceae, Myristicaceae, and Palmae. In a review of 44 floristic inventories (62.34 ha) of várzea forests scattered over the Amazon basin, Wittmann et al. (2006a) stated that the Fabaceae were the most important várzea tree family, followed by the Malvaceae (including former Bombacaceae, Sterculiaceae, and Tiliaceae), Euphorbiaceae, Moraceae, Palmae, and Salicaceae (including former Flacourtiaceae) (Table 4.1; the classification is the angiosperm phylogeny group, APG II 2003). The family importance, however, depends strongly on the location of the forest along the flood-level gradient, the successional stage, and the geographic location of the inventories.

Independent of vertical or geographic gradients the 18 most important tree families account for about 80–90% of all várzea tree species; however, the distribution of várzea tree families differs considerably between low-várzea and high-várzea forests. Specifically, the Fabaceae, Malvaceae, Salicaceae, Urticaceae, and Brassicaceae are more important in low-várzea forests, whereas Euphorbiaceae, Moraceae, Palmae, Annonaceae, Meliaceae, and Myristicaceae are more important in high-várzea forests (Table 4.1). Along the longitudinal gradient, Sapotaceae, Rubiaceae, Polygonaceae, and Clusiaceae are of increasing importance from eastern Amazonia to western Amazonia, whereas Malvaceae and Salicaceae show an opposite trend. Fabaceae, Euphorbiaceae, Urticaceae, Brassicaceae, Lauraceae, and Verbenaceae are more important in central Amazonia than in eastern and western várzea forests. Finally, there are also variations in family importance along the latitudinal gradient: Fabaceae, Euphorbiaceae, Urticaceae, and Lecythidaceae are more important in equatorial western Amazonia, whereas Malvaceae, Moraceae, Palmae, and Meliaceae are more important in the southern part of western Amazonia (Table 4.1).

4.2.2.2 Floristic Patterns at the Species Level

With more than 1,000 recorded tree species, Amazonian várzea forests are the most species-rich floodplain forests worldwide and thus reflect the high diversity patterns generally characterizing the neotropical flora (Wittmann et al. 2006a). Species richness

Table 4.1 Family distribution of the 18 most important várzea tree families along vertical and geographic gradients. Numbers represent percentages of total importance values (TIV, Curtis and McIntosh 1951)

	Family	Vertical distribution		Longitudinal distribution			Latitudinal distribution in WA	
		LV	HV	EA	CA	WA	WAe	WAs
1	Fabaceae	12.46	8.45	7.62	12.23	8.79	10.05	6.9
2	Malvaceae	12.45	8.34	30.54	14.09	6.88	4.5	10.45
3	Euphorbiaceae	7.35	8.47	4.37	8.41	7.34	8.49	5.63
4	Moraceae	5.67	11.42	5.74	5.51	11.8	9.44	15.34
5	Arecaceae	5.09	12.33	5.58	0.71	11.42	9.36	14.5
6	Salicaceae	6.73	1.99	11.94	6.62	4.14	3.51	5.02
7	Urticaceae	5.23	2.53	4.63	5.69	3.21	4.68	1.02
8	Annonaceae	3.79	5.49	1.4	3.98	4.23	4.74	3.47
9	Brassicaceae	5.06	0.17	3.98	6.21	0.13	0.14	0.12
11	Lauraceae	3.92	1.24	2.18	4.72	1.16	1.62	0.47
12	Lecythidaceae	3.13	1.95	2.91	2.28	3.46	5.42	0.54
13	Verbenaceae	3.70	0.25	2.3	4.53	0.21	–	0.52
14	Meliaceae	1.41	5.09	1.02	0.52	4.99	3.65	6.99
15	Myristicaceae	0.9	4.76	1.75	1.08	3.8	4.64	2.53
16	Rubiaceae	1.7	2.28	1.16	1.78	2.36	2.93	1.52
17	Polygonaceae	2.48	2.19	2.06	2.44	2.77	2.77	1.77
18	Clusiaceae	1.89	1.28	1.11	1.15	2.28	1.25	3.82
Total		86.3	82.22	91.91	85.01	82.66	80.4	85.03
No. of families		63	64	35	48	64	56	44

LV, low várzea; HV, high várzea; EA, eastern Amazonia; CA, central Amazonia; WA, western Amazonia; WAe, equatorial western Amazonia; WAs, southern part of western Amazonia in the Amazonian várzea is at least 20 times higher than in the floodplains of the European temperate zone (Schnitzler et al. 2005) and about ten times higher than in the subtropical bottomland forests of North America (Johnson and Little 1967; Clark and Benforado 1981; Schnitzler et al. 2005). Compared with tropical floodplains, species richness in the Amazonian várzea is about ten times higher than in the forests of Cambodia (Tonle Sap; Campbell et al. 2006) and about three times higher than in the Brazilian Pantanal (Junk et al. 2006). One reason for the comparatively high tree species richness in várzea forests is the coexistence of species well-adapted to flooding and generalist species that also occur in the uplands.

At the species levels, the floristic similarity (SI, Sørensen's 1948 index) between várzea and adjacent terra firme forests amounts to about 30% for trees ≥10 cm dbh in all parts of the Amazon basin (see Terborgh and Andresen (1998) for the western part of the basin, Gama et al. (2005b) for the eastern part of the basin, and Wittmann et al. (2006a) for the central part of the basin) and to approximately 34% for trees ≥5 cm dbh (F. Wittmann, 2006, unpublished data; from terra firme originate from Oliveira and Mori 1999; Ribeiro et al. 1999; Pitman et al. 2001 and Gama et al. 2005b), because the latter comparison includes the mostly small trees and shrubs of families such as Melastomataceae, Theophrastaceae, and Burseraceae.

At the basin-wide scale (918 tree species in 62.34 ha), the 30 most important low-várzea species account for 42.3% of the overall importance (OI = sum of the importance value index (IVI; Curtis and McIntosh 1951) and the relative frequency [rF] in 44 inventories scattered over the Amazon basin [Wittmann et al. 2006a]), whereas the 30 most important high-várzea species account for only 24.9% of the OI (Table 4.2). Floristic similarity between low-várzea forests and high-várzea forests is 35% in eastern Amazonian várzea (data from Cattanio et al. 2002), but only 17.5% in central Amazonian várzea (Wittmann 2001; Wittmann et al. 2002b). For the western part of the basin, no data allowing for a comparison between low várzea and high várzea are available.

Low-várzea forests exhibit high floristic similarities, even when separated by large geographic distances. SI between adjacent low-várzea forest inventories may be as high as 70% (Wittmann et al. 2006a). With increasing distance between sites, floristic similarity decreases. Nevertheless, the SI between low-várzea forests >1,000 km apart still averages about 20% and exceeds 40% in several cases (Fig. 4.11), whereas comparative studies indicate that it averages less than 10% between low-várzea forests and the adjacent terra firme (Wittmann et al. 2002b, 2006; Fig. 4.12).

SI between adjacent high-várzea forests is about 30%, but decreases linearly to less than 10% in plots >1,000 km apart (Wittmann et al. 2006a; Fig. 4.13). We have estimated that species similarity of high-várzea forests and adjacent terra firme forests is between 25% and 32% (Fig. 4.12). Terborgh and Andresen (1998) previously concluded that geographic position is an important driver of floristic dissimilarity in both terra firme and alluvial floodplain forests. The authors found that within a region mean similarity between terra firme and flooded forests is larger than within forests of terra firme and floodplain respectively of two different regions. Thus, tree communities of inundated forests tend to more closely resemble those of terra firme forests within the same geographical region than those of inundation forests in

Table 4.2 Overall importances of the 30 most-important species in (a) low várzea and (b) high várzea. rIVI = relative importance value index (Curtis and McIntosh 1951), rF = relative frequency (a: n = 34 plots; b: n = 18 plots), OIV = overall importance value (= IVI + rF in 44 inventories scattered over the Amazon basin (Wittmann et al. 2006a)

	Family	Species	rIVI	rF	OIV
(a)					
1	Malvaceae	*Pseudobombax munguba* (Mart. & Zucc.) Dugand	8.48	1.47	9.95
2	Salicaceae	*Laetia corymbulosa* Spruce ex Benth.	5.33	1.18	6.51
3	Brassicaceae	*Crataeva benthamii* Eichler	5.13	0.97	6.10
4	Urticaceae	*Cecropia latiloba* Miq.	4.51	1.19	5.70
5	Fabaceae	*Pterocarpus amazonum* (Mart. ex Benth.) Amshoff	3.23	1.26	4.49
6	Verbenaceae	*Vitex cymosa* Bert. ex Spreng.	3.76	0.56	4.32
7	Lauraceae	*Nectandra amazonum* Nees	3.11	1.05	4.16
8	Euphorbiaceae	*Piranhea trifoliata* Baill.	2.73	0.98	3.71
9	Malvaceae	*Luehea cymulosa* Spruce ex Benth.	2.90	0.70	3.60
10	Arecaceae	*Euterpe oleracea* Mart.	2.67	0.56	3.23
11	Moraceae	*Ficus trigona* L.f.	2.40	0.42	2.82
12	Polygonaceae	*Triplaris surinamensis* Cham.	1.46	0.70	2.16
13	Bignoniaceae	*Tabebuia barbata* (E. Mey.) Sandwith	1.16	0.98	2.14
14	Fabaceae	*Macrolobium acaciifolium* (Benth.) Benth.	1.16	0.91	2.07
15	Aquifoliaceae	*Ilex inundata* Poepp. ex Reissek	1.67	0.29	1.96
16	Lecythidaceae	*Eschweilera albiflora* (DC.) Miers	1.37	0.56	1.93
17	Fabaceae	*Vatairea guianensis* Aubl.	1.13	0.77	1.90
18	Moraceae	*Maclura tinctoria* (L.) D. Don ex Steud.	1.20	0.63	1.83
19	Arecaceae	*Astrocaryum chonta* Mart.	1.18	0.42	1.60
20	Euphorbiaceae	*Mabea nitida* Spruce ex Benth.	0.96	0.56	1.52
21	Sapotaceae	*Pouteria elegans* (DC.) Baehni	1.02	0.42	1.44
22	Euphorbiaceae	*Hevea spruceana* (Benth.) Müll.Arg.	0.98	0.42	1.40
23	Rubiaceae	*Duroia duckei* Huber	0.83	0.56	1.39
24	Bignoniaceae	*Crescentia amazonica* Ducke	0.96	0.42	1.38

	Family	Species	rIVI	rF	OIV
25	Lecythidaceae	*Eschweilera parvifolia* Mart. ex DC.	0.90	0.42	1.32
26	Lecythidaceae	*Gustavia augusta* L.	0.40	0.91	1.31
27	Myrtaceae	*Calyptranthes crebra* Mc Vaugh	0.85	0.35	1.20
28	Clusiaceae	*Calophyllum brasiliense* Cambess	0.63	0.56	1.19
29	Salicaceae	*Casearia aculeata* Jacq.	0.61	0.56	1.17
30	Myristicaceae	*Virola surinamensis* (Rol. ex Rottb.) Warb.	0.48	0.63	1.11
Σ			63.20	21.41	84.61
Σ 31–617			36.80	78.59	115.39
Total			100	100	200
(b)					
1	Moraceae	*Brosimum lactescens* (S. Moore) C.C. Berg	2.56	0.80	3.36
2	Malvaceae	*Theobroma cacao* L.	1.83	0.65	2.48
3	Euphorbiaceae	*Hura crepitans* L.	1.65	0.58	2.23
4	Meliaceae	*Trichilia septentrionalis* C. DC.	1.82	0.29	2.11
5	Anacardiaceae	*Spondias lutea* L.	1.59	0.51	2.10
6	Moraceae	*Maquira coriacea* (H. Karst.) C.C. Berg	1.53	0.51	2.04
7	Arecaceae	*Astrocaryum chonta* Mart.	1.64	0.36	2.00
8	Boraginaceae	*Cordia nodosa* Lam.	1.20	0.73	1.93
9	Arecaceae	*Iriartea deltoidea* Ruiz & Pav.	1.46	0.44	1.90
10	Euphorbiaceae	*Drypetes amazonica* Steyerm.	1.49	0.36	1.85
11	Arecaceae	*Euterpe oleracea* Mart.	1.04	0.65	1.69
12	Euphorbiaceae	*Alchornea triplinervia* (Spreng.) Müll. Arg.	1.49	0.15	1.64
13	Malvaceae	*Ceiba samauma* (Mart.) K. Schum.	1.24	0.36	1.60
14	Dichapetalaceae	*Tapura acreana* (Ule) Rizzini	1.36	0.22	1.58
15	Myristicaceae	*Otoba parvifolia* (Markgr.) A.H. Gentry	1.40	0.15	1.55
16	Meliaceae	*Guarea macrophylla* Vahl	1.07	0.44	1.51

(continued)

Table 4.2 (continued)

	Family	Species	rIVI	rF	OIV
17	Rubiaceae	*Calycophyllum spruceanum* (Benth.) Hook.	1.06	0.44	1.50
18	Arecaceae	*Attalea phalerata* Mart. ex Spreng.	1.23	0.22	1.45
19	Moraceae	*Ficus maxima* Mill.	1.00	0.44	1.44
20	Euphorbiaceae	*Sapium marmieri* Huber	0.79	0.65	1.44
21	Arecaceae	*Astrocaryum jauari* Mart.	0.98	0.44	1.42
22	Annonaceae	*Unonopsis floribunda* Diels	0.73	0.58	1.31
23	Arecaceae	*Scheelea brachyclada* Burret	1.23	0.07	1.30
24	Polygonaceae	*Coccoloba densifrons* C. Mart. ex Meisn.	0.79	0.51	1.30
25	Malvaceae	*Ceiba pentandra* (L.) Gaertn.	0.81	0.44	1.25
26	Myristicaceae	*Virola calophylla* (Spruce) Warb.	0.72	0.51	1.22
27	Violaceae	*Leonia glycycarpa* Ruiz & Pav.	0.64	0.58	1.22
28	Myristicaceae	*Virola cuspidata* (Spruce ex Benth.) Warb.	0.60	0.58	1.18
29	Myristicaceae	*Virola surinamensis* (Rol. ex Rottb.) Warb.	0.81	0.36	1.17
30	Moraceae	*Pseudolmedia laevis* (Ruiz & Pav.) J.F. Macbr.	0.73	0.44	1.17
Σ			36.49	13.46	49.94
Σ 31–686			63.51	86.54	150.06
Total			100	100	200

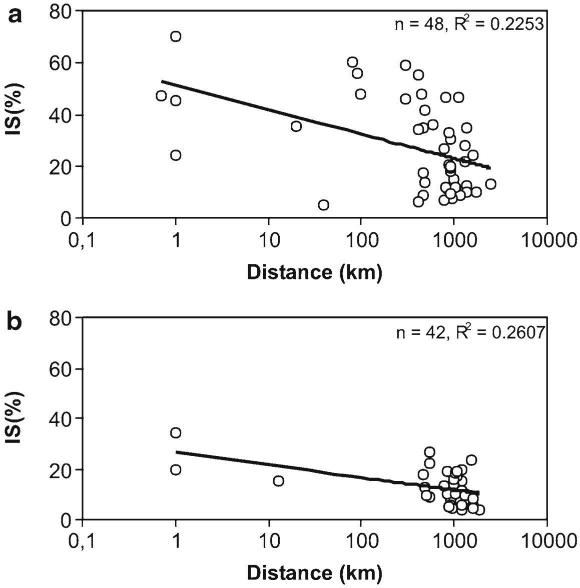

Fig. 4.11 Floristic similarity (IS = Sørensen's 1948 Index) between low-várzea forests (**a**) and high-várzea forests (**b**) over geographic distance (trees ≥10 cm dbh in floristic inventories totaling 62.34 ha (Wittmann et al. 2006a)

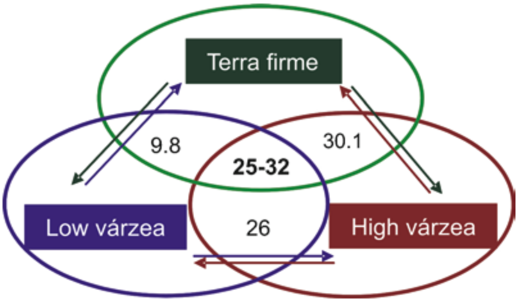

Fig. 4.12 Basin-wide floristic similarity (IS = Sørensen's 1948 Index) between low-várzea forests, high-várzea forests, and terra firme forests. Data from várzea originate from Wittmann et al. (2006a); data from terra firme originate from Ribeiro et al. (1999), Oliveira and Mori (1999), Oliveira and Nelson (2001), Pitman et al. (2001) and Duque et al. (2002)

adjacent regions. This holds true for the high várzea, where intense lateral species exchange between the high várzea and the terra firme is likely to occur (Wittmann and Junk 2003). Tree species of the terra firme migrate to the nutrient-rich floodplains and may establish in the high várzea, where inundations are short. The establishment of terra firme species in low-várzea forests, by contrast, requires long-term development of physiological or morphological adaptations to the periodic flooding events.

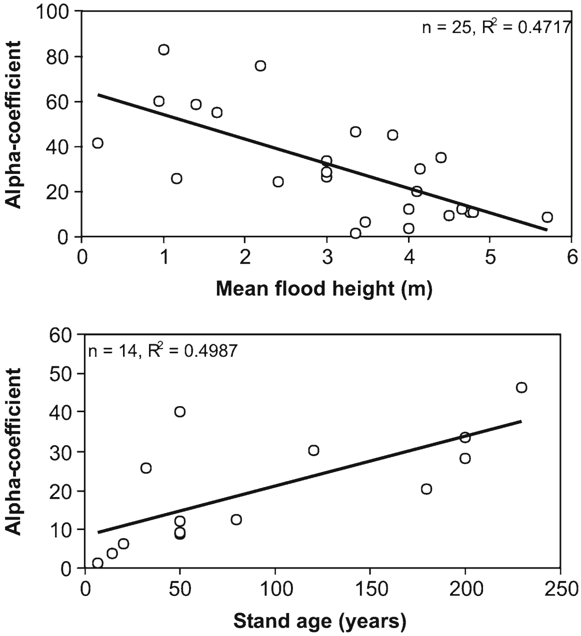

Fig. 4.13 Fisher's alpha-diversity coefficient (Fisher et al. 1943) plotted against mean flood height (**a**) and mean stand age (**b**) of várzea forest plots (Wittmann et al. 2006a)

The SI between várzea forests in eastern Amazonia and those in the western regions is approximately 20%. It increases to about 32% between central Amazonia and equatorial western Amazonia, about 31% between central Amazonia and the southern part of western Amazonia, and reaches the highest percentage between equatorial western Amazonia and the southern part of western Amazonia (about 36%, Wittmann et al. 2006a). The 30 overall most important tree species (OI = low-várzea + high-várzea forests) account for 30.4% and 46.0% of all species recorded in eastern Amazonia and central Amazonia, respectively, but only for 13.5% in equatorial western Amazonia and 20% in the southern part of western Amazonia (Wittmann et al. 2006a). This indicates that the floristic composition in the western Amazonian várzea is distinctly different from that in the eastern regions.

Tree species richness and alpha-diversity (Fisher et al. 1943) of várzea forests are significantly correlated with flood height and length as well as with the age of the forest stand (Fig. 4.13). The maximum species richness (≥10 cm dbh) recorded in high-várzea forests of eastern Amazonia is 84 species ha^{-1} (Cattanio et al. 2002), with 142 species ha^{-1} in central Amazonia (Wittmann et al. 2002b), and 157 species ha^{-1} in the southern part of western Amazonia (Dallmeier et al. 1996). These values show that maximum species richness in várzea forests is 60–70% of that of adjacent upland forests (117–120 species ha^{-1} in eastern Amazonia, 179–285 species ha^{-1} in central Amazonia, and up to 300 species ha^{-1} in western Amazonia (Gentry 1987; Valencia et al. 1994; data summarized from Oliveira and Nelson 2001; see also Ter Steege et al. 2003; Fig. 4.14).

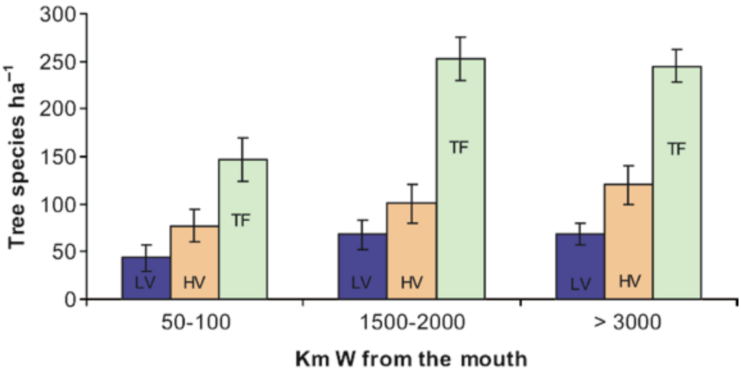

Fig. 4.14 Mean species richness in low-várzea forests (LV), high-várzea forests (HV), and terra firme forests (TF) as a function of the distance from the inventories to the mouth of the Amazon River. Data from várzea originate from Wittmann et al. (2006a), data from terra firme forests originate from Gentry (1987), Valencia et al. (1994), Ribeiro et al. (1999), Oliveira and Mori (1999), Oliveira and Nelson (2001), Pitman et al. (2001), and Ter Steege et al. (2003)

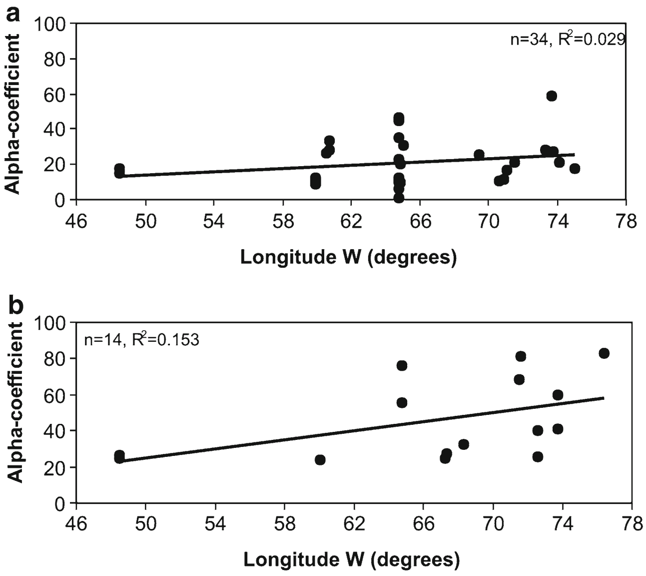

Fig. 4.15 Fisher's alpha-diversity coefficient (Fisher et al. 1943) plotted against the longitudinal location of the plots in low várzea (**a**) and high várzea (**b**) (Wittmann et al. 2006a)

Alpha-diversity and the longitudinal location of the forests are significantly correlated, indicating a trend of increasing diversity from east to west (Wittmann et al. 2006a). This trend is moderately pronounced in high-várzea forests but weak in low-várzea forests (Fig. 4.15). Within western Amazonian várzea forests, alpha-diversity decreases from equatorial western Amazonia to the southern part of western Amazonia. Again, this trend is more pronounced within high-várzea forests (n = 10 floristic inventories, $R^2 = 0.4898$, $P < 0.001$) than in low-várzea forests (n = 4 floristic inventories, $R^2 = 0.0223$, $P < 0.05$).

A trend of increasing alpha-diversity from east to west was also documented for equatorial Amazonian terra firme, where it seems to be linked to tree density and rainfall seasonality (e.g., Condit et al. 2000, 2002; Pitman et al. 2002; Ter Steege et al. 2003). Nonetheless, a recent study instead indicated that the nutrient status of the soil is the most important factor influencing diversity gradients from eastern to western terra firme (Ter Steege et al. 2006). Within várzea forests, increasing diversity from east to west is especially pronounced within the high várzea. We have argued that, in addition to the intense lateral species exchange between high várzea and terra firme, the high alpha-diversity in western Amazonian várzea is the result of the high nutrient status originating from poorly weathered alluvial substrates compared with that further east. The strong floristic resemblance between high várzea and terra firme is especially pronounced in western Amazonia, because of the more accentuated topography compared to the relief of floodplains further east. Inundations in western Amazonia are higher but shorter than those in central and eastern Amazonia (Terborgh and Andresen 1998). Therefore, trees without specific adaptations to flooding might establish more readily in western Amazonian várzea.

4.2.2.3 Species Oligarchies, Endemism and the Tree Species Colonization Concept

The periodic flood pulse associated with the hydrogeomorphologic dynamism of várzea floodplains implies that the ecological factors important for the establishment and distribution of tree species in várzea forests are relatively constant over thousands of kilometers along the river courses. Describing the abundance patterns of tree species at different scales in Peru and Ecuador, Pitman et al. (2001) stated that the majority of the most abundant tree species found in floristic inventories in Amazonian terra firme belong to a small set of ubiquitous, common tree species that combine high frequency with local abundance, thus forming predictable oligarchies that dominate over vast areas (several thousand square kilometers) of forest at each site. The authors further argued that these species distribution patterns are more indicative of regulation of relative abundances by ecological factors than by non-equilibrium chance-based dynamics (*sensu* Hubbell and Foster 1986; Hubbell 1995) or by the patchiness and unpredictability of tropical forest landscapes, as described by Denslow (1987), Gentry (1988), and Clark et al. (1995, 1998).

We have proposed that species oligarchies in várzea forests are even more evident than in the terra firme, where edaphic changes at different spatial scales may influence species distribution patterns (e.g., Tuomisto et al. 1995; Terborgh and Andresen 1998). Despite the small-scale heterogeneity of the alluvial landscape, the high connectivity of riparian corridors leads to similar, vertically arranged ecological niches across remote várzea forests and, consequently, to a restricted number of highly dominant tree species across the Amazon basin (Wittmann et al. 2006a). Godoy et al. (1999)

noted that the Amazon and Orinoco basins show marked similarities in habitats and tree species, which the authors interpreted as being the result of the high connectivity between the riparian corridors of the two basins and the effective operation of dispersal mechanisms. Long-distance dispersal by currents and fish is common for many low-várzea trees (Gottsberger 1978; Goulding 1983; Pires and Prance 1985; Ziburski 1991; Kubitzki and Ziburski 1994; Lopez 2001; Moegenburg 2002; Mannheimer et al. 2003; Scarano et al. 2003; Oliveira Wittmann et al. 2007a) and thus contributes to randomly distributed tree species that dominate several thousands of square kilometers in Amazonian várzea.

Kubitzki (1989) stated that many floodplain tree species are ecotypes originating from the surrounding terra firme. When the species immigrated to the floodplains, they gradually developed adaptations to the periodic inundations. The colonization of episodically flooded margins of small rivers (igarapés) in the terra firme, or general high precipitation with persistent soil saturation might be an important prerequisite in the provision of a transitional habitat for terra firme species migrating to the floodplains. Once they tolerate and/or create specific adaptations to episodic inundations, these species are able to colonize the higher parts of the floodplains, where inundations are low, sometimes occasional, and do not exceed about 50 days year^{-1}. Wittmann and Junk (2003) stated that the number of immigrant species from the adjacent terra firme is highest within the low-flooded high várzea. Some of these species developed to species able to colonize the lower parts of the floodplains, where periodic waterlogging of roots, parts of the above-ground organs, or the entire plant is unavoidable. With an increasing water column and inundation period, natural selection led to only a few species, i.e., those able to tolerate the extreme inundations near the forest border. At this stage, we have argued, species colonization is driven by the selection pressure provided by flooding and the associated hydrogeomorphologic factors. Effective competitive mechanisms lead to a stage in which an ecotype reaches a 'point of no return', which means that it has developed adaptations to the periodic inundations that no longer allow successful competition in non-flooded environments. Following our tree species colonization concept (Fig. 4.16), the ecotype thus became endemic to the floodplains.

Despite the fact that distribution maps of most Amazonian tree species are incomplete due to the patchiness of botanical collecting and the scarcity of forest inventories in combination with the huge geographic area, some authors have concluded that Amazonian floodplain forests are characterized by a high degree of endemic tree species (Prance 1979; Kubitzki 1989; Junk 1989). Endemism can be defined as 'the restriction of a genotype to a defined geographic region, without taking into consideration its size' (Ricklefs 1990; Schroeder 1998). Haeupler (1983) suggested the term 'micro-scale endemism' for species with a restricted occurrence in very small areas, such as islands or inselbergs. For tropical forests, Gentry (1986) proposed the term 'local endemism' to describe genotypes restricted to areas <75,000 km^2.

We investigated the occurrence and distribution of the 186 most common tree species of central Amazonian várzea, using the species samples available in the literature (62.34 ha scattered over the Amazon basin, Wittmann et al. 2006a), herbaria (Instituto Nacional de Pesquisas da Amazonia (INPA), Manaus, Brazil;

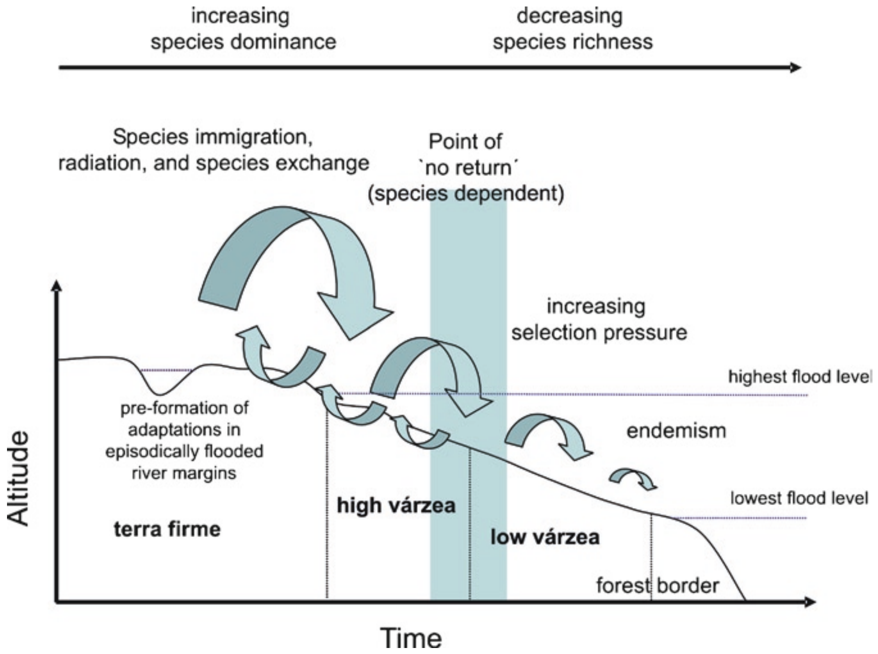

Fig. 4.16 Species colonization concept in várzea floodplains

Missouri Botanical Garden (MBG), USA; New York Botanical Garden (NYBG), USA; Royal Botanical Gardens, Kew, Great Britain), and the Internet (including specimens available in digital herbaria databases such as the *Flora Brasiliensis* (Martius 1840–1906), the National Herbarium of Utrecht, the Netherlands, the International Legume database (Ildis), etc.). The results indicated that 74 (39.78%) of the 186 most common central Amazonian várzea tree species can be classified as endemics following the definition of Ricklefs (1990). Of these endemic tree species, the occurrence of 50 (67.56%) of them was restricted to the low várzea, while 11 (14.86%) were present in both low-várzea and high-várzea forests, and only 13 (17.57%) were restricted to high-várzea forests (Table 4.3).

The results of our investigation further indicated that 112 (60.21%) of the most frequent central Amazonian várzea tree species are generalist species that also occur in other neotropical ecosystems. Prance (1979) and Worbes (1997) stated that some of these generalist tree species (e.g., *Pseudobombax munguba*, *Leonia glycycarpa* Ruiz & Pav., and *Duroia duckei*) are widely distributed throughout the neotropics and occur particularly in semi-deciduous forests and savannas. Our investigation, however, showed that, of the 186 most common tree species of the central Amazonian várzea, only 12 (6.45%; mostly Malvaceae and Fabaceae) occur in ecosystems with climatic- and/or edaphic-induced aridity, such as the Cerrado, the Caatinga, or the Pacific (western) slope of the Andes. Twenty-seven (12.90%) várzea species also occur in southeastern Brazilian Atlantic rainforests. The majority of Amazonian várzea tree species are found in adjacent moist terra firme forests

Table 4.3 Number of endemic species (*sensu* Ricklefs 1990) and generalist species within the 186 most common várzea tree species of the Amazon basin. (*sensu* Wittmann et al. 2006a; see text for explanation and data source)

	Number of species	(%)
Investigated várzea tree species	186	100.00
Endemic to Amazonian várzea	74	39.78
Endemic to Amazonian low várzea	50	26.88
Endemic to Amazonian high várzea	13	6.99
Occurrence in other neotropical ecosystems	112	60.22
Occurrence in moist terra firme	100	53.76
Occurrence in moist terra firme and igapó	36	19.35
Occurrence in Amazonian igapó	21	11.29
Occurrence in Central America and the Caribbean	59	31.72
Ocurrence in savanna (Cerrado, Caatinga, Llanos, Chaco)	12	6.45
Occurrence in Atlantic rainforest	27	14.52
Occurrence in the Paleotropis	6	3.23

(100 tree species, 53.76%). Only 21 (18.75%) are restricted to várzea and igapó, whereas 36 (32.14%) occur in all Amazonian ecosystems, i.e., várzea, igapó, and moist terra firme forests (Table 4.3).

Our data thus indicate that species oligarchies *sensu* Pitman et al. (2001) are common in Amazonian várzea forests. The oligarchies are the feature of two different species groups: (1) generalist species of high-várzea forests that also occur in the surrounding terra firme, and to a lesser extent in other neotropical ecosystems, e.g., the igapó, the Atlantic rainforest, and cerrados and caatingas [many of these species, inlcuding *Ceiba pentandra* (L.) Gaertn. and *Leonia glycycarpa*, are included in Pitman's list of ubiquitous species]; and (2) endemic species (*sensu* Ricklefs 1990) of low-várzea forests, which dominate thousands of square kilometers along the river courses. We estimated that about one-third of these endemic low-várzea tree species (e.g., *Crescentia amazonica* Ducke, *Clitoria amazonum* Mart. ex Benth.) are present in spatially restricted areas along the main tributaries of the Solimões and Amazon Rivers and thus can be classified as local endemics *sensu* Gentry (1986).

A discussion of species oligarchies and endemism in várzea forests must also focus on the floristic evolution of neotropical floodplain and upland forests. Evidence of the occurrence of tropical rainforests in South America dates from at least the early Paleocene (Burnham and Graham 1999; Rull 1999; Johnson and Ellis 2002; Burnham and Johnson 2004). Pollen data from Colombia, Guyana, and Venezuela lend support for warm, equable climates at low altitudes in the early Paleocene (Van der Hammen and Wymstra 1964; Van der Hammen and Garcia 1966; Colmenares and Teran 1993; Jaramillo and Dilcher 2000, 2001), while climatic reconstructions for the Eocene, based on global climate modeling (Frakes et al. 1992; Beerling and Woodward 2001; Ziegler et al. 2003), indicate tropical temperatures encompassing from one-third to two-thirds of the South American continent. Paleobotanically based reconstructions have shown that tropical rainforests in the Eocene extended uninterruptedly from southern Bolivia to New Mexico (Frakes et al. 1992; Burnham and Johnson 2004).

Theoretically, the tropical climate in equatorial Amazonia together with the continuous uplift of the Andes would have already created the physical conditions for the development of várzea forests beginning in at least the early Paleocene. This geological time span certainly was sufficiently long enough to allow for specific adaptations of ecotypes to important ecological factors in floodplain forests and thus to species dominance and oligarchy. With respect to Neogene and Quaternary landscape histories, and despite the impact of climatic changes especially during the last glacial maximum (LGM) and the controversially discussed refugia hypothesis, there is no evidence for forest fragmentation in equatorial Amazonia during the glacial periods (Colinvaux et al. 2000; Van der Hammen and Hooghiemstra 2000; Colinvaux and De Oliveira 2001; Anhuf et al. 2006). Instead, the impact of a drier climate during the LGM affected the equatorial lowland forest on the species level rather than on the community level, i.e., by shifting species sensitive to soil-moisture seasonality to comparatively wet refuges, and by the occurrence of now montane species in the lowlands (Bush et al. 1990; Colinvaux et al. 2000; Oyama and Nobre 2004; Hutyra et al. 2005).

It is, nonetheless, indubitable that climatic changes during the tertiary and quaternary directly affected the sea level and thus the size of floodplain forests by periodic reductions (during the LGM) and enlargements (during the interglacials, formation of the Lago Amazonas) of their areas (Vuilleumier 1971; Van der Hammen 1974; Frailey et al. 1988; Tuomisto et al. 1992; Irion et al. 1995, 1997; Oliveira and Mori 1999). The postulated species shift from dry to moist climatic conditions combined with a spatial reduction of flooded areas, however, affected floodplain species to a lesser extent than upland species, because the flooded ecosystems persisted, at smaller scales, even during glacial maximums. The riparian connectivity and the highly adapted dispersal mechanisms of floodplain trees would have reduced species losses at regional scales (Wittmann 2001), with the floodplains themselves acting as linear refuges for sensitive terra firme species during periods with postulated dryer climatic conditions (Pires 1984). Due to the constant habitat availability even through tertiary and quaternary climatic changes, species oligarchies in várzea forests are evident.

4.3 The Igapó Forest

Much less phytogeographic knowledge is available for the Amazonian igapó than for the várzea floodplains. The majority of floristic inventories in igapó forests were carried out in central Amazonia, at the lower Negro River near Manaus (Rodrigues 1961; Takeuchi 1962; Keel and Prance 1979; Revilla 1981; Worbes 1986; Ferreira 1991; Parolin et al. 2004; Ferreira and Almeida 2005), or at the same river, about 150 km NW in the Jaú National Park (Ferreira 1997, 2000; J. Schöngart et al. 2005, unpublished). Further central Amazonian igapó inventories were done by Ayres (1993) and Inuma (2006) in the Amanã Sustainable Development Reserve, near the city of Tefé, and by Haugaasen and Peres (2006) at small blackwater rivers near the confluence with the lower Purús River. From the eastern Amazonian igapó, there are three floristic inventories, one by Campbell et al. (1986) at the Xingú River, one by Ferreira and Prance (1998) at the lower Tapajós River, and one by Ferreira et al. (2005) at the Curuá River, about 400 km east of the city of Belém. From the western and northwestern Amazon basin, no published floristic inventories in igapó forests are available.

Tree species composition and diversity in igapó forests are linked to the location of forest types along the flooding gradient in the same range as in várzea forests. The closed forest border, however, occurs at sites where mean inundation is 9.0–9.5 m (corresponding to an inundation period of 280–290 days year^{-1}; Schlüter 1989; Ferreira 1997). The establishment of the forest border at different flood levels in the várzea and igapó can be explained through photon flux under water during aquatic phases. Sunlight is transmitted in black-water and clear-water to depths of 2.0–2.5 m, whereas in white-water it is transmitted only to depths of 0.3–0.5 m (Sioli 1984b; Furch and Junk 1997a). The duration and height of flooding as well as the water chemistry thus form a light-incidence threshold for tree seedlings and define the elevations where trees can successfully establish. Furthermore, smaller amounts of easily degradable organic material result in anoxic conditions in the water, near the bottom, for shorter periods in igapó forests than in the várzea.

Several authors noted different patterns of tree species composition and richness along the flooding gradient in igapó forests of the lower Negro River (Worbes 1986, 1997; Ferreira 1997, 2000). In a floristic inventory of 1 ha of each of several igapó forests of the Jaú National Park, at elevations where the mean inundation height is 8.6 ± 0.5 m, 4.8 ± 0.3 m, and 2.1 ± 0.7 m, Ferreira (1997) recorded 44, 103, and 137 tree species ≥10 cm dbh, respectively. J. Schöngart et al. (2005, unpublished) noted seven tree species ≥10 cm dbh in an area of 625 m^2 in an igapó forest of the Jaú National Park subjected to a mean inundation of 6.55 m, whereas in plots of the same sizes but where the inundation height was 1 m and 1.9 m, 12 and 14 tree species, respectively, were reported. Investigating tree species richness and diversity of trees ≥5 cm dbh in inventories of 0.2-ha areas in three different elevations (4.8, 2.2, and 1.0 m) at the lower Rio Negro near Manaus, Ferreira (2000) described a significant increase of species richness and diversity with decreasing height of inundation. Inuma (2006) confirmed this relationship in floristic inventories at three different inundation levels, each with an area of 0.75 ha, in igapó forests of the Lago Amanã. Tree species richness ≥10 cm increased from 26 species at inundation levels between 7 and 5 m, to 35 and 44 species at inundation levels of 5–3 m and 3–1 m, respectively.

The zonation of tree species along the flooding gradient and the increase of species richness with decreasing impact of flooding appear also to be linked to the physical conditions of the soil. In general, igapó soils are coarser than várzea soils (Irion et al. 1997; Haugaasen and Peres 2006). Several authors observed white-sand soils in low-lying igapó tree communities (Piedade 1985; Worbes 1986; Ferreira 1997), while the soils of higher-lying communities consisted of at least 50% clay (Worbes 1986, 1997). Highly flood-tolerant tree species that dominate white-sand igapó soils in central Amazonia include *Borreria capitata* (Ruiz & Pav.) DC., *Dalbergia inundata* Spruce ex Benth., *Pithecellobium* spp., and *Eugenia* spp., while those of higher elevations and clayish soils include *Couepia paraensis* (Mart. & Zucc.) Benth. ex Hook f., *Leopoldinia insignis* Mart., and *Licania* spp. (Worbes 1997; Ferreira 2000). Detailed species lists of igapó forests on the different soil types, as recorded in inventories carried out by Keel and Prance (1979), Revilla (1981), Piedade (1985), Worbes (1986), and Ferreira (1991), were provided by Worbes (1997).

To date, the comparatively few floristic inventories available in igapó forests do not allow for a reliable classification of different stand age classes and/or successional stages or forest types, which complicates, among other things, comparisons of forest structure between várzea and igapó. Ferreira (1997) reported a significant increase in tree densities (≥10 cm dbh), from 796 to 941 and 1,130 trees ha^{-1}, with decreasing impact of flooding, from 8.6 to 4.8 and 2.1 m, respectively, in igapó forests of the Jaú National Park. However, the basal area of the three elevations appears to be characterized by the same distribution as in várzea forests (for comparison with várzea, see Fig. 4.6). Highly flooded igapó forests show comparatively low basal areas (20–22 m^2 ha^{-1}, 8.6 m flood height). The highest basal areas were recorded in mid-level flood communities (about 41 m^2 ha^{-1}, 4.8 m flood height), whereas in higher-located communities basal areas declined again (about 34 m^2 ha^{-1}, 2.1 m flood height; Ferreira 1997).

The increase in densities of trees ≥10 cm dbh with decreasing impact of flooding in igapó forests contrasts with the situation in várzea forests, where tree densities generally decline from highly flooded to low flooded sites, becoming highest in early-secondary stages (Worbes et al. 1992; Schöngart 2003; Wittmann et al. 2004). Other authors found no significant differences in tree densities ≥10 cm dbh in comparative studies of várzea and igapó forests at the lower Purús River and the Amanã Sustainable Development Reserve (Haugaasen and Peres 2006; Inuma 2006). Increasing tree densities with decreasing flood height were later described by Ferreira (2000) at the lower Negro River, near Manaus, for trees ≥ 5 cm dbh. An increase in the tree density of small trees and saplings with increasing topographic elevation of the forested sites was also documented for várzea forests (Wittmann and Junk 2003).

Species richness comparisons between várzea and igapó forests in the vicinity of the city of Manaus (Worbes 1986, 1997) and at the Floresta National de Caxiuanã (Caruá River, Ferreira et al. 2005) indicated higher species richness in igapó forests. These studies, however, compared forest communities of different successional stages and topographic levels, but gave no information about the degree of anthropogenic disturbance, particularly in the várzea. By contrast, Prance (1979, 1987) and Ayres (1993) stated that igapó forests are generally poorer in tree species than várzea forests. The highest species richness (≥10 cm dbh) reported from igapó was 137 species ha^{-1} in a forest subjected to inundations of 2.1 m (Ferreira 1997). This value is below the maximum species richness described by Balslev et al. (1987), Dallmeier et al. (1996), Nebel et al. (2001), and Wittmann et al. (2002a,b) in western and central Amazonian high-várzea forests. That species richness is lower in the igapó than in the várzea was recently confirmed by comparative floristic studies from Haugaasen and Peres (2006) at the lower Purús River and from Inuma (2006) in the Amanã Sustainable Development Reserve. Ongoing floristic inventories in the igapó forests of the Amanã Reserve also indicate lower species richness in the igapó than in the várzea of the nearby located Mamirauá Sustainable Development Reserve (Schöngart et al. 2005) (Figs. 4.17 and 4.18).

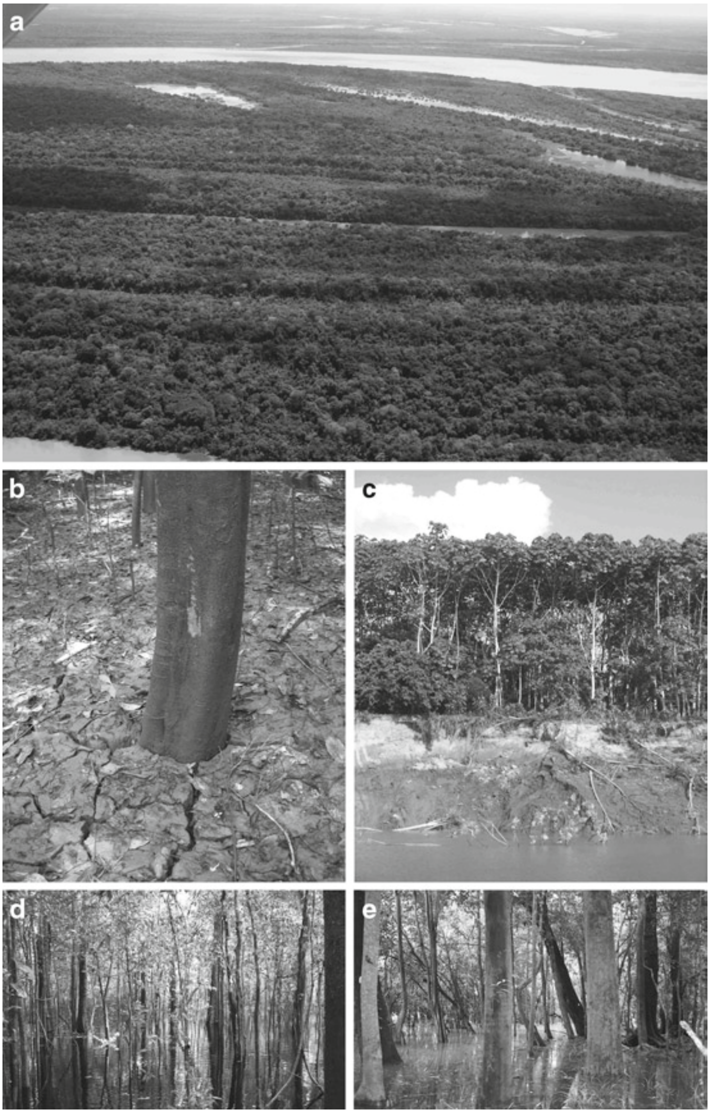

Fig. 4.17 (**a**) Mamirauá Sustainable Development Reserve, between the Japurá (*top*) and the Solimões Rivers: The sediment of the major Amazonian white-water rivers is deposited in form of meanders, channel-bars, depressions, and lakes, which partially loose connection to the main-river channels during the low-water periods. (**b**) High annual sedimentation rates cover the superficial root layer of an individual of *Pseudobombax munguba* at a fluvial island next to the Japurá River bank. Besides the creation of anoxia at the root level of mature trees, the sediment destroys tree regeneration at these sites. (**c**) Solimões River near the city of Tefé: Independent of the successional stage of the forest stand, fluvial erosion can destroy several hectares of forest during one high-water period. (**d**) Lower Purús River near the city of Beruri: Late-secondary stages are composed by tree species with maximum ages between 80 and 150 years. These forests are characterized by densities of 500–600 individuals ha^{-1}, belonging to 20–50 tree species. (**e**) Mamirauá Sustainable Development Reserve, near the community of São Raimundo do Jarauá: Low-várzea late-successional stages are well-stratified and colonized by trees with maximum ages of up to 400 years. Due to annual inundations of up to 3 m in height, the sub-canopy stratum is characteristically poor in individuals

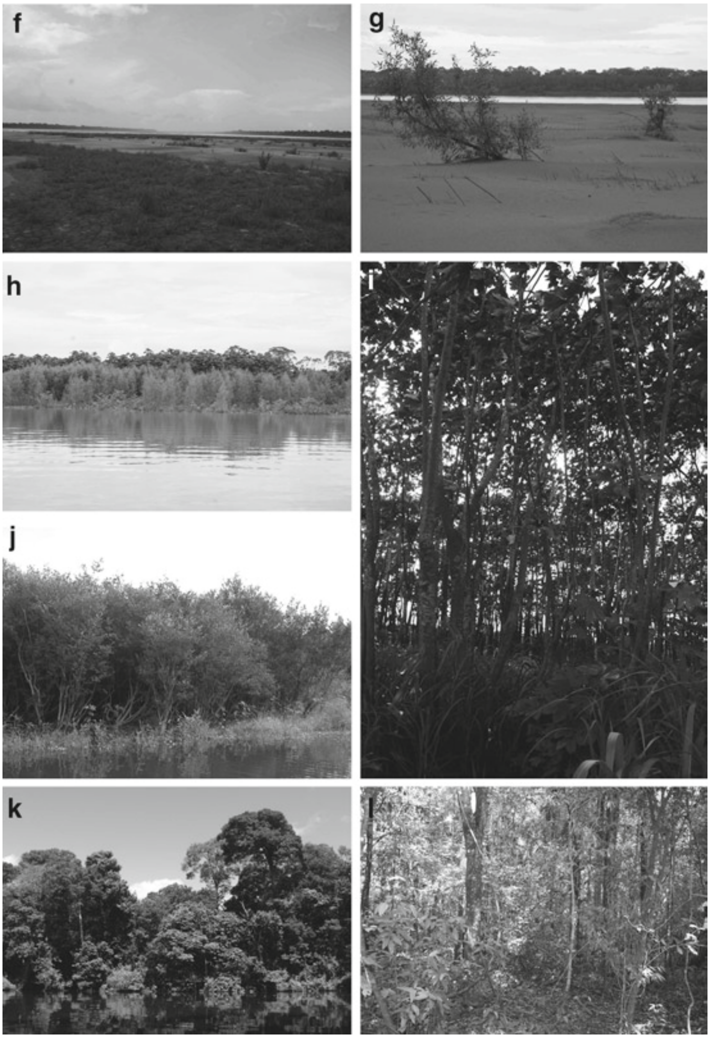

Fig. 4.18 (**f**) Japurá River, Mamirauá Sustainable Development Reserve: Large-scale new-site colonization by annual grasses that establish during the terrestrial phases. These grasses are frequently replaced by perennial grasses (mainly *Paspalum respens* and *Echinochloa polystachya*), which in turn decrease water energy and favour the deposition of sediment, allowing for the establishment of pioneer tree species. (**g**) Solimões River near the city of Manaus: When sediment is deposited at topographic levels subjected to less than 7.5 m of inundation (corresponding to a flooded period of <270 days year^{-1}), first pioneer trees like *Alchornea castaneifolia* establish without prior colonization by grasses. (**h**): Solimões River near the city of Manaus: Monospecific stand of the pioneer tree *Salix martiana*. Besides inundations of up to 7 m in height, and 100% of rPAR, this species tolerates high sedimentation rates due to the formation of secondary root layers above the annual sediment deposits. (**i**) Japurá River, Mamirauá Sustainable Development Reserve: The perennial grasses *Paspalum repens* and *Echinochloa polystachya* are replaced by the

The scarcity of floristic inventories in clear-water floodplain forests do not allow reliable comparisons with black-water and white-water floodplain forests concerning species composition, richness, and diversity. Ferreira and Prance (1998) recorded 21, 24, and 30 tree species ha^{-1} (≥5 cm dbh) in a floristic inventory totaling 3 ha in clear-water forests at the lower Tapajós River near Santarém. Campbell et al. (1986) recorded 40 tree species ≥10 cm dbh in an area of 0.5 ha in clear-water forests of the Xingú River. Both inventories were done in forests on white-sand soils and were thus comparable to inventories of highly flooded igapó forests of the Negro River (Ferreira 1997). Besides flooding and nutrient scarcity, Ferreira and Prance (1998) argued that the low species richness found at the lower Tapajós River could be the result of the surrounding savanna vegetation, which is generally poorer in tree species than is the case for the upland forests surrounding the igapó of the Negro River. Kubitzki (1989) and Ferreira and Prance (1998) noted high floristic similarities between Amazonian clear-water and black-water forests, and cited several tree species that are found on white-sand soils in both forest ecosystems (e.g., *Swartzia polyphylla* DC., *Campsiandra laurifolia* Benth., *Cynometra spruceana* Benth., *Leopoldinia insignis*, *Burdachia prismatocarpa* A. Juss., and *Macrolobium multijugum* (DC.) Benth.). However, 16 of the 36 tree species found by Ferreira and Prance (1998) at the lower Tapajós River also were reported to occur in Amazonian white-water floodplains (data from Wittmann et al. 2006a). More detailed comparisons can only be obtained when data from additional floristic inventories in black-water and clear-water igapó forests are available.

The igapó forests of the lower Negro River are characterized by a distinct species composition. Differences between igapó of the Negro River and the central Amazonian várzea already can be detected at the family level. Fabaceae, Euphorbiaceae, Sapotaceae, and Lecythidaceae are important families in both forest ecosystems, but with significantly greater importance in the igapó. Malpighiaceae, Combretaceae, and Ochnaceae, which are among the ten most important families in igapó, are of very little importance in várzea forests. By contrast, Malvaceae,

Fig. 4.18 (continued) tree species *Cecropia latiloba*, which form monospecific and dense stands with densities of up to 1,000 individuals ha^{-1}. After the creation of a closed canopy, the light-demanding C_4-grasses swiftly loose competition by shading. When the trees reach ages of about 20 years, *C. latiloba* itself no longer regenerates at this site, and will be replaced by species of late-secondary stages. (**j**) Maciel lake, Mamirauá Sustainable Development Reserve: *Eugenia ochrophloea* is one of highly flood-tolerant tree species that colonizes the margin of still-water systems in oxbows and lakes. At these sites, sedimentation rates are reduced, and the fine-grained substrate and the accumulated organic material often cause anaerobic site conditions during the most part of the year. (**k**) Secondary-river channel Paracuúba, Mamirauá Sustainable Development Reserve: With more than 100 species ha^{-1}, high-várzea forests are the most species-rich várzea forest type, which is characterized by emergent trees with maximum heights of up to 40 m. These forests establish along the elevated banks of rivers and river channels. (**l**) Secondary-river channel Paracuúba, Mamirauá Sustainable Development Reserve: The lower stratum of high-várzea forests is densely covered by shrubs, small trees, and tree regeneration competing for light

Table 4.4 Comparison of importance (FIV = relative abundance + relative dominance) of the 17 most important families (trees ≥10 cm dbh) in central Amazonian igapó (mean values of inventories totaling 3 ha in the Jaú National Park, Rio Negro; Ferreira 1997) and central Amazonian várzea (mean values of inventories totaling 3 ha in the Mamirauá Sustainable Development Reserve, Solimões River, Wittmann et al. 2002b).

	Igapó	Várzea
Fabaceae	28.14	12.23
Euphorbiaceae	20.89	8.41
Malvaceae	<1	14.09
Sapotaceae	6.46	3.06
Salicaceae	2.19	6.62
Moraceae	2.48	5.51
Malpighiaceae	7.44	<1
Lecythidaceae	4.46	2.28
Combretaceae	6.13	<1
Brassicaceae	<1	6.21
Annonaceae	1.93	3.98
Urticaceae	<1	5.69
Myrtaceae	3.45	2.14
Lauraceae	<1	4.72
Chrysobalanaceae	3.32	1.31
Verbenaceae	<1	4.53
Ochnaceae	2.81	<1

Salicaceae, Moraceae, Brassicaceae, Urticaceae, and Lauraceae belong to the ten most important várzea families, but are not particularly important within igapó forests (Table 4.4).

At the species levels, floristic similarities between central Amazonian várzea and the igapó of the lower Negro River amount to about 32%. Parolin et al. (2004) found that, based on two inventories performed at the lower Negro River near the confluence with the Solimões River, one 0.1 ha (trees ≥3.2 cm dbh), and the other 1.5 ha (trees ≥32 cm dbh), only about 30% of the 44 tree species had restricted occurrence in igapó. The majority of species occurred in igapó, várzea, and the surrounding terra firme.

Using floristic data from central Amazonian várzea, summarized by Wittmann et al. (2006a), and from our species list of the 186 most common tree species in central Amazonian várzea (see Section 2.2), and from the igapó species lists summarized by Worbes (1997), Ferreira (1997), Ferreira and Prance (1998) and Parolin et al. (2004), we compiled a species list of common tree species in igapó and várzea (Table 4.5). The greater portion of species found in both ecosystems also was reported in the surrounding uplands.

Table 4.5 Most common tree species occurring in igapó forests of the lower Negro River and of the lower Tapajós River, and in Amazonian várzea forests. Data from our study concerns the 186 most common várzea tree species found in central Amazonian várzea; data from Wittmann et al. (2006a) concern species in 44 inventories (62.34 ha) across the Amazon basin. (1) Ferreira (1997), (2) Ferreira and Prance (1998), (3) Ferreira (2000), (4) Parolin et al. (2004), (5) Worbes (1997), (6) Haugaasen and Peres (2006), (7) Wittmann et al. (2006a), and (8) our study

Species	Ocurrence in igapó	Occurrence in várzea
Acosmium nitens (Vogel) Yakovlev	2	8
Alibertia edulis (Rich.) A. Rich. ex DC.	1	8
Buchenavia oxycarpa (Mart.) Eichler	1	8
Byrsonima amazonica Griseb.	3	8
Caryocar microcarpum Ducke	4	8
Couepia paraensis (Mart. & Zucc.) Benth.	2, 5	8
Crudia amazonica Spruce ex Benth.	1	8
Eschweilera albiflora (DC.) Miers	4	7, 8
Eschweilera parvifolia Mart. ex DC.	3	7, 8
Hevea spruceana (Benth.) Müll.Arg.	1, 3	7, 8
Inga punctata Willd.	1, 3	8
Licania apetala (E. Mey.) Fritsch	2	8
Licania heteromorpha Benth.	4	8
Mabea nitida Spruce ex Benth.	3	7, 8
Macrolobium acaciifolium (Benth.) Benth.	1, 2	7, 8
Malouetia tamaquarina (Aubl.) A.DC.	1, 3	8
Mouriri guianensis Aubl.	1	8
Myrciaria dubia (Kunth) McVaugh	2	8
Ormosia excelsa Benth.	1	8
Piranhea trifoliata Baill.	5, 6	7, 8
Pouteria elegans (A.DC.) Baehni	1, 3, 4	7, 8
Quiina rhytidopus Tul.	3	8
Swartzia polyphylla DC.	1, 3	8
Tabebuia barbata (E. Mey.) Sandwith	2, 5	7, 8
Unonopsis guatterioides (A. DC.) R.E. Fries	3	8

4.4 Conclusions

The information provided in this chapter demonstrates that Amazonian floodplain forests belong to special ecosystems with a partial highly adapted and endemic vegetation. The flood pulse and the ecologic connectivity created by the vast and dynamic Amazonian river system allow for simultaneous ecological processes and predictable aggregations of tree species over huge geographic distances. Tree species richness and diversity variations and species oligarchies in Amazonian floodplains seem to follow environmental gradients and rules similar to those of Amazonian terra firme. Although increasing attention has been focused on the floristic variation within forests of the Amazon Basin, species composition and diversity variations are still poorly understood. There are large Amazonian floodplain areas for which no floristic information is available, i.e., along the tributaries of the Solimões/Amazon Rivers and in Amazonian igapó. We are thus still at the beginning of our efforts to describe the Amazonian floodplain flora and to understand the evolutionary and ecological interactions between floodplains and their surrounding uplands.

Slight changes of the atmospheric water content beginning in the early Paleocene were probably crucial factors triggering the evolution of both Amazonian floodplain and terra firme forests. More comparative studies between floodplain and terra firme forests thus would not only close local gaps in species distribution maps, but might also reveal important results that allow for interpretations of the evolution and current state of Amazonian flora as a whole. We are therefore convinced that these kinds of studies will substantially contribute to an understanding and modeling of the Amazonian flora with respect to present and future climate changes.

Part II
Ecological and Ecophysiological Aspects of Amazonian Floodplain Forests

Chapter 5
Tree Phenology in Amazonian Floodplain Forests

Pia Parolin, Florian Wittmann, and Jochen Schöngart

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Abstract The flood pulse operates as a regulator for the timing of phenological events, the phenology of Amazonian floodplain tree species is linked to the seasonal water-level changes. Many tree species shed and resprout leaves during the high-water season. Flowering and fruiting reach their peaks during the aquatic phase. However, with the present knowledge, there is still a discussion about the possible triggers which are responsible for these phenological events. Long-term studies of several years are lacking, and the results presented by various authors are not directly comparable. Inter- and intraspecific variations at all levels along the flood gradient, and between várzea and igapó, are frequent. Many Amazonian floodplain tree species occur in non-flooded ecosystems where phenology is triggered by precipitation, drought, solar irradiance, and temperature. It is possible that these factors act also in the floodplains, but the extent is not clear.

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5.1 Introduction

The flood pulse is the main driving force which is predictable and responsible for the existence, the productivity and the interactions of the biota in the floodplains (Junk et al. 1989). This implies that flooding also operates as a regulator for the timing of phenological events. Phenology in many Amazonian floodplain tree species is linked to the seasonal water-level changes. Many tree species shed and resprout leaves during the high-water season and flowering and fruiting reach its peaks during the aquatic phase especially in highly flooded species. However, with the present knowledge, there is still a discussion about the possible triggers which are responsible for these phenological events.

Qualitative descriptions of the phenology of Amazonian floodplain species exist which are focused mainly on specific aspects of reproductive phenology (Ziburski 1991; Nebel et al. 2001b) or linked to vegetation analyses (Revilla 1991; Ferreira 1991). In many cases leaf phenology was studied either unspecifically and quantitatively to determine litter production (Adis et al. 1979; Franken et al. 1979; Nebel et al. 2001a; Schöngart et al. 2010) or to describe the habitat of herbivores (Ayres 1993; Queiroz 1995; Haugaasen and Peres 2005). Quantitative measurements of vegetative phenology have seldom been performed (but see Wittmann and Parolin 1999; Schöngart et al. 2002). With the exception of a 5-year study on the flowering phenology of *Ceiba pentandra* (Gribel et al. 1999), a 2-year study of 23 species in central Amazonia (Schöngart et al. 2002), and a 3-year study in central-western Brazilian Amazonia with 400 trees in várzea and 400 in igapó (Haugaasen and Peres 2005), continuous recordings over many years are almost completely lacking (but see Table 5.1).

The first continuous recordings were made in a 2-year study by Revilla (1981). He dealt with six tree communities at Praia Grande, a black-water floodplain of the Negro River near Manaus. This study showed that flooding can act as a regulating factor for phenology in some species, but there was a high diversity in the timing of phenological events in the six communities, with evergreen, semi-deciduous, and deciduous species which flush their leaves before, during or after flowering, when the water receded, or at high water (see Table 5.2). The same diversity was documented by Ferreira (1991) who analysed 30 tree species in an igapó community of the Rio Tarumã-Mirim near Manaus. The phenological cycles were not necessarily triggered by the flood periodicity, as indicated by monitoring trees growing at different elevations in the flooding gradient (Ferreira 1991, 1998). There was a high inter- and intraspecific diversity of phenological traits in the analysed igapó community, which was found also when comparing pioneer and non-pioneer species of the várzea (Worbes 1983; Parolin 1997; Wittmann 1997; Oliveira 1998; Armbrüster 1999; Wittmann and Parolin 1999). The only homogeneous trait among the floodplain trees is the period of fruit maturation, which is during high water or at the end of the flooded period, linked to dispersal by water or fish, as documented by Ziburski (1990) for 33 tree species. Schöngart et al. (2002) found that in different functional ecotypes, phenology showed a periodic behaviour mainly triggered by the flood pulse.

Table 5.1 Studies with continuous phenological observations performed in central Amazonia, in chronological order, with study sites, species, and number of individuals per species (n)

Author, year of publication	Study sites	Species n per species	Duration of phenol recordings
Revilla (1981)	Igapó: Praia Grande/Negro River near Manaus	37 species n = 3 per species	20 months (4/1978–11/1979)
Piedade (1985)	Igapó: Negro River (Anavilhanas Archipelago)	*Astrocaryum jauari*	12 months (1981)
Ziburski (1990)	Várzea: Marchantaria Island near Manaus	18 species in várzea	16 months (1/1988–4/1989)
	Igapó: Tarumã Mirim, Praia Grande, Negro River near Manaus	15 species in igapó	
Ferreira (1991)	Igapó: Tarumã Mirim near Manaus	30 species n = 15–19 per species	12 months (5/1989–5/1990)
Worbes (1996)	Várzea: Marchantaria Island near Manaus	7 species	12 months? (1981/82)
Parolin (1997)	Várzea: Costa do Catalão, Ilha de Marchantaria near Manaus	6 species; n = 5 per species	15 months (4/1994–6/1995)
Maia (1997)	Igapó: Tarumã Mirim near Manaus	*Eschweilera tenuifolia, Hevea spruceana* n = 15	18 months (7/1993–12/1994)
Wittmann (1997)	Várzea: Ilha de Marchantaria near Manaus	6 species n = 2	4 months (6/1996–9/1996)
Ferreira (1998)	Igapó: Tarumã Mirim near Manaus	*Eschweilera parvifolia* n = 24	12 months (5/89–5/90)
Oliveira (1998)	Várzea: Ilha de Marchantaria and Rio Solimões near Manaus	*Salix humboldtiana* (= *S. martiana*) n = 75	14 months (4/1993–5/1994)
Armbrüster (1999)	Várzea: Ilha de Marchantaria near Manaus	*Laetia corymbulosa, Pouteria glomerata* n = 1	11 months (4/1997–6/1998)

(continued)

Table 5.1 (continued)

Author, year of publication	Study sites	Species n per species	Duration of phenol recordings
Gribel et al. (1999)	Várzea: Costa do Catalão near Manaus	*Ceiba pentandra* n = 12	5 years (1992–1997)
Schöngart et al. (2002)	Várzea: Ilha de Marchantaria near Manaus	23 species; n = 66 individuals	2 years (06/1998–08/2000)
Haugaasen and Peres (2005)	Várzea, igapó and terra firme on the lower Purús (central-western Brazilian Amazonia)	126 genera; n = 400 individuals per ecosystem (1,200 in total)	3 years (08/2000–11/2003)

Table 5.2 Central Amazonian tree species with vegetative phenology (Veg Phen; D, deciduous; BD, Brevi-deciduous; E, evergreen), elevation at which they mainly grow in the flooding gradient (high = 25–28 m asl, low = 18–25 m asl), and floodplain type (Fl. type), updated from Parolin et al. (2002)

Species	Family	Veg. phen.	Elev.	Fl. type	Reference
Acosmium nitens	Fabaceae	D	L	I	Revilla (1981)
Albizia multiflora	Fabaceae	D	L	V	Schöngart et al. (2002)
Alchornea castaneifolia	Euphorbiaceae	BD	L	V	Parolin pers. obs., Schöngart et al. (2002)
Alchornea schomburgkiana	Euphorbiaceae	D	L?	I	Revilla (1981)
Aldina latifolia	Fabaceae	D	H	I	Revilla (1981); Ziburski (1990); Ferreira (1991)
Aniba affinis	Lauraceae	E?	–	I	Ziburski (1990)
Annona hypoglauca	Annonaceae	–	L	V	Ziburski (1990)
Annona sp.	Annonaceae	–	–	V	Ziburski (1990)
Annona sp.	Annonaceae	BD	L	V	Schöngart et al. (2002)
Astrocaryum jauari	Arecaceae	E	L	V + I	Piedade (1985); Ziburski (1990)
Banara guianensis	Salicaceae	E	L	I	Ferreira (1991)
Bonafusia tetrastarhya	Apocynaceae	E	L	V	Worbes (1996)
Buchenavia ochnopnuma	Combretaceae	D	L	I	Revilla (1981)
Buchenavia oxycarpa	Combretaceae	D?	L?	V	Ziburski (1990)
Buchenavia suaveolens	Combretaceae	D	L?	I	Revilla (1981)
Burdachia prismatocarpa	Malpighiaceae	D	–	I	Revilla (1981)
Byrsonima chrysophylla	Malpighiaceae	E	–	I	Revilla (1981)
Calophyllum brasiliense	Clusiaceae	E	L/H	V	Schöngart et al. (2002)
Campsiandra comosa	Fabaceae	D	L	I	Revilla (1981); Ziburski (1990)
Caryocar microcarpum	Caryocaraceae	E	L	I	Ferreira (1991)
Cecropia latiloba	Urticaceae	E	L	V	Ziburski (1990); Parolin (1997); Wittmann (1997); Schöngart et al. (2002)
Cecropia membranacea	Urticaceae	E	H	V	Parolin, personal observation

(continued)

Table 5.2 (continued)

Species	Family	Veg. phen.	Elev.	Fl. type	Reference
Ceiba pentandra	Malvaceae	D	H	V	Gribel et al. (1999)
Clitoria amazonum	Fabaceae	D	L	V + I	Parolin, personal observation
Cordia sp.	Boraginaceae	D	L	V	Schöngart et al. (2002)
Couepia paraensis	Chrysobalanaceae	D/E	L	I	Revilla (1981); Ferreira (1991)
Crataeva benthamii	Brassicaceae	D	L	V	Ziburski (1990); Worbes (1996); Parolin (1997); Schöngart et al. (2002)
Crescentia amazonica	Bignoniaceae	D	L	V	Ziburski (1990); Worbes (1996)
Crudia amazonica	Fabaceae	D	L	I	Ziburski (1990)
Elaeoluma glabrescens	Sapotaceae	E	–	V	Worbes (1983)
Elvasia calophyllum	Ochnaceae	D	L	I	Revilla (1981)
Eschweilera coriacea	Lecythidaceae	D	–	I	Revilla (1981)
Eschweilera ovalifolia	Lecythidaceae	E	L	V	Ziburski (1990); Schöngart et al. (2002)
Eschweilera parvifolia	Lecythidaceae	E	H + L	I	Ferreira (1998)
Eschweilera tenuifolia	Lecythidaceae	E	L	I	Ziburski (1990); Maia (1997)
Eugenia cachoerensis	Myrtaceae	E	–	I	Revilla (1981)
Eugenia inundata	Myrtaceae	D	L	V + I	Parolin, personal observation
Eugenia longiracemosa	Myrtaceae	D	–	I	Revilla (1981)
Eugenia tefensis	Myrtaceae	D	–	I	Revilla (1981)
Euterpe precatoria	Arecaceae	E	H	V	Kahn and Henderson (1999)
Genipa spruceana	Rubiaceae	D	L	V	Parolin, personal observation
Gustavia augusta	Lecythidaceae	E	L	V	Schöngart et al. (2002)
Hevea spruceana	Euphorbiaceae	BD	L	I	Maia (1997)
Himatanthus attenuata	Apocynaceae	D	L?	I	Revilla (1981)
Humiria balsamifera	Humiriaceae	E	H?	I	Revilla (1981)
Ilex inundata	Aquifoliaceae	E	L	I	Parolin, personal observation

Ilex sp.	Aquifoliaceae	D	L?	V	Worbes (1983)
Laetia corymbulosa	Salicaceae	E	L	V	Ziburski (1990); Wittmann (1997); Armbrüster (1999); Schöngart et al. (2002)
Laetia suaveolens	Salicaceae	D	L	I	Revilla (1981); Ziburski (1990)
Leopoldinia pulchra	Arecaceae	E	L	I	Revilla (1981)
Licania apetala	Chrysobalanaceae	D	L	I	Revilla (1981)
Luehea cymulosa	Malvaceae	BD	L	V	Schöngart et al. (2002)
Macrolobium acaciifolium	Fabaceae	BD!	L	V + I	Ziburski (1990); Worbes (1996); Schöngart et al. (2002)
Macrolobium multijugum	Fabaceae	D	L	I	Revilla (1981); Ziburski (1990)
Maprounea guianensis	Euphorbiaceae	D/E	L	I	Revilla (1981); Ferreira (1991)
Mollia speciosa	Malvaceae	E	H	I	Revilla (1981)
Mora paraensis	Fabaceae	D	H	I	Ziburski (1990)
Myrciaria dubia	Myrtaceae	D	L	I	Revilla (1981); Ziburski (1990)
Nectandra amazonum	Lauraceae	E	L	V	Ziburski (1990); Parolin (1997); Wittmann (1997); Schöngart et al. (2002)
Neolabatia cuprea	Sapotaceae	–	–	V	Ziburski (1990)
Ormosia excelsa	Fabaceae	E	L	I	Ziburski (1990)
Ouratea spruceana	Ochnaceae	E	H?	I	Revilla (1981)
Palicourea nitidella	Rubiaceae	E	–	I	Revilla (1981)
Parkia auriculata	Fabaceae	E	L	I	Ferreira (1991)
Parkia discolor	Fabaceae	D	L	I	Revilla (1981)
Piranhea trifoliata	Euphorbiaceae	BD	L	V	Worbes (1996); Schöngart et al. (2002)
Pithecellobium adiantifolium	Fabaceae	D	L	I	Revilla (1981); Ziburski (1990)

(continued)

Table 5.2 (continued)

Species	Family	Veg. phen.	Elev.	Fl. type	Reference
Pithecellobium amplissimum	Fabaceae	E	L	I	Ferreira (1991)
Pithecellobium inaequale	Fabaceae	–	L?	V	Ziburski (1990)
syn. Zygia inaequalis	Fabaceae	E	L	V	Schöngart et al. (2002)
Platymiscium ulei	Fabaceae	E?	H	V	Parolin pers. obs.
Pouteria glomerata	Sapotaceae	E	L	V	Armbrüster (1999); Schöngart et al. (2002)
Pouteria stylosa	Sapotaceae	–	L?	V	Ziburski (1990)
Pseudobombax munguba	Malvaceae	D	L	V	Ziburski (1990); Worbes (1996); Wittmann (1997); Schöngart et al. (2002)
Psidium acutangulum	Myrtaceae	D	L	V	Ziburski (1990); Wittmann (1997); Schöngart et al. (2002)
Pterocarpus amazonum	Fabaceae	D	L	V	Schöngart et al. (2002)
Garcinia brasiliensis	Clusiaceae	E	L	V	Ziburski (1990); Schöngart et al. (2002)
Garcinia floribunda	Clusiaceae	E	L?	I	Revilla (1981)
Salix martiana	Salicaceae	E	L	V	Oliveira (1998)
Sclerolobium hypoleucum	Fabaceae	D	–	I	Revilla (1981)
Senna reticulata	Fabaceae	E	H	V	Parolin (1997)
Simaba guianensis	Simaroubaceae	D	–	I	Revilla (1981)
Simaba obovata	Simaroubaceae	E	–	I	Revilla (1981)
Simaba orinocensis	Simaroubaceae	E	H	I	Ziburski (1990)
Sorocea duckei	Moraceae	–	L	V	Ziburski (1990)
Swartzia argentea	Fabaceae	E	L	I	Ferreira (1991)
Swartzia laevicarpa	Fabaceae	E	L	I	Revilla (1981)
Swartzia polyphylla	Fabaceae	E	H	I	Revilla (1981); Ziburski (1990)

Swartzia sericea	Fabaceae	D	–	I	Revilla (1981)
Symmeria paniculata	Polygonaceae	D?	L	I	Revilla (1981)
Tabebuia barbata	Bignoniaceae	D	L	V + I	Revilla (1981); Ziburski (1990); Ferreira (1991); Parolin (1997); Schöngart et al. (2002)
Tabernaemontana juruana	Apocynaceae	E	L	V	Parolin, personal observation
Triplaris surinamensis	Polygonaceae	BD	L	V	Worbes (1983); Schöngart et al. (2002)
Triplaris weigeltiana	Polygonaceae	E?	H	V	Ziburski (1990)
Vatairea guianensis	Fabaceae	D	L/H	V + I	Parolin, personal observation, Schöngart, personal observation
Vitex cymosa	Verbenaceae	D	L	V	Ziburski (1990); Worbes (1996); Parolin (1997); Wittmann (1997); Schöngart et al. (2002)
Xylopia aromatica	Annonaceae	D	–	I	Revilla (1981)

In the present chapter, we summarize the knowledge of phenological studies performed in Amazonian floodplain forests. We focus on common and diverging phenological patterns observed in both várzea and igapó, and on intra- and interspecific variability along the flooding gradient. Finally, we discuss the possible triggers for tree phenology in this peculiar environment.

5.2 Statements and Hypotheses

Comparisons and syntheses of the available studies to postulate general statements and hypotheses are problematic, because they were performed in different years with variations in the constellation of external climate factors such as precipitation and inundation, in different forest ecosystems with varying stand ages (successional stages), contrasting nutrient status (várzea vs. igapó) and differences in the length of inundation (flood gradient).

Based on these studies and further observations of single species, some general statements and hypotheses concerning the timing and triggers of phenological events in central Amazonian floodplains can be found in the literature:

1. Leaves are shed mainly in the first half of the aquatic phase (Worbes 1983; Revilla 1991; Ayres 1993; Schöngart et al. 2002; Haugaasen and Peres 2005), especially in the low várzea, where most species shed their leaves in June and July, or even earlier (Schöngart et al. 2002), when the river levels are at their peak. In the species from igapó, the period of leaf shedding is more towards the end of the flooded period and the beginning of the terrestrial period (September and October), which is congruent with the statements of Revilla (1981) and Worbes (1997) that in the igapó a maximum of shedding occurs in the end of the flooded period. However, the study of Haugaasen and Peres (2005) does not support this difference between igapó and várzea.
2. New leaves are mainly flushed when the forests are still flooded (Worbes 1997; Wittmann and Parolin 1999). A second leaf flush can be observed in the dry season before the onsets of rains (Schöngart et al. 2002) which appears more distinct for evergreen species and less distinct for deciduous species. One can infer from the decrease in leaf shedding that the species from várzea flushed new leaves in August and September, towards the end of the flooded period, whereas in igapó many leaves were flushed at high water (July, August), but the peak of leaf flush was in November and December, in the non-flooded period. Again, these findings are not supported by Haugaasen and Peres (2005).
3. Flowering occurs mainly at the beginning of the flooded period (Worbes 1997). In várzea, there is a peak of flowering in May and June (Schöngart et al. 2002), i.e. at highest water levels. In igapó many trees had flowers in February when the flood begins, but there was a rapid decrease of flowering in March and April. However, Haugaasen and Peres (2005) showed that flowering in the igapó and várzea peaks in October and there are no differences between the ecosystems.

4. Fruits are produced mainly in the flooded period (Worbes 1986; Ziburski 1990; Ayres 1993; Haugaasen and Peres 2005), as an adaptation to water and fish dispersal (Ziburski 1991; Goulding 1983). This is true in both várzea and igapó, although in central Amazonia the peak of fruiting in várzea (June–July) occurs later than in igapó (February–April).

There are very few long-term studies which compare annual cycles and allow the determination of triggers (Schöngart et al. 2002). Most of the tree species are restricted to very small topographic amplitudes along the flooding gradient (Wittmann et al. 2002a,b; Wittmann et al. 2010). Thus, only few studies (Ferreira 1991; Schlüter and Furch 1992; Ferreira 1998; Ayres 1993) compared species at different elevations in the flooding gradient, but these also do not give clear insights into the role of flooding as trigger. The amount of deciduousness among tree species colonizing low flooded sites (high-várzea *sensu* Wittmann et al. 2002a,b) seems to be lower than the amount of deciduousness in species colonizing the high flooded sites (low várzea) (Pia Parolin obs.). About 40% of várzea tree species were estimated to be endemic, most of them restricted to the low várzea (Wittmann et al. 2010).We thus argue that the majority of low-várzea species developed adaptations to long-term inundations, and reduce its metabolism resulting in pronounced leaf shedding during the aquatic phases. High-várzea tree species developed fewer adaptations to flooding, and phenology of many species thus may be triggered by direct climatic induced factors (e.g. precipitation, radiation).

5.3 Vegetative Phenology

In Amazonian floodplain forests, some species like *Symmeria paniculata* maintain their leaves below water in absolute darkness for up to 5 years without damage (Fig. 5.1; Junk pers. comm.). Other species shed their leaves when submerged (Fig. 5.2), indicating a high diversity of phenological performances among the tree species despite the striking flooding events (Fig. 5.3). The timing of leaf shedding and leaf flush, and the duration of the leafless period, are closely related to flooding (Parolin et al. 2002c; Schöngart et al. 2002). In seasonally dry regions like savannas, trees shed their leaves and reduce the production of new leaves in a period of dry conditions (Reich and Borchert 1982; Bullock and Solís-Magallanes 1990; Wright and Cornejo 1990; Gribel et al. 1999). This pattern is described as a strategy of ‘drought-avoidance’ (Medina 1983). In floodplains, the flooding can – but does not in many species – disturb the root function, i.e. water uptake, and reduces the water status of a tree (Gill 1970; Kozlowski 1984a,b; Meyer 1991; Blom and Voesenek 1996). In fact, the leafless period often begins at highest water levels in the first half of the aquatic phase, and lasts until the end of flooding, or until the terrestrial period in igapó (e.g. until November in *Parkia discolor*, *Sclerolobium hypoleucum* and *Simaba guianensis*, Parolin et al. 2002). Worbes (1992) found that most tree species had a cambial rest during this period which leads to the formation of annual tree rings (Worbes and Fichtler 2010). The period of regular growth

Fig. 5.1 *Symmeria paniculata* (Polygonaceae) after emersion (November 1994, Rio Jaú; Pia Parolin)

Fig. 5.2 The deciduous tree species *Vitex cymosa* (Verbenaceae) remains bare during the high water period (May 2006, Reserva de Desenvolvimento Sustentável Piagaçu-Purus; Jochen Schöngart)

Fig. 5.3 Flooded igapó forest with trees displaying different phenologies at high water (August 1995, Paraná Ariaú; Pia Parolin)

reductions corresponded to the period of maximum leaf fall (Schöngart et al. 2002). The same observation led Gessner (1968) to the concept of the 'physiological winter' hypothesis, where he states that flooding represents a stress factor for trees like winter in temperate regions, and leaves are shed to cope with the unfavourable environmental conditions. However, the high phenological and physiological activity during the flooded period (Schlüter 1989; Schlüter et al. 1993; Parolin 1997; Maia 1997; Armbrüster 1999) does not support this statement. Several studies have shown that flooding does not impede high photosynthetic rates, which are reduced only for a short part of the flooded phase, and are often linked to leaf senescence (Maia 1997; Parolin 1997). High stem water potential enables trees to flush leaves, to flower, and to produce fruits (during the time of high water stress; Schöngart et al. 2002).

If flooding has an influence which is comparable to the temperate winter, we would expect leaves to be shed at the beginning of the aquatic phase and not be produced again until the end of flooding. A second peak of leaf shedding can occur in the non-flooded period in October (Schöngart et al. 2002), when precipitation is very low (about 50 mm per month) and leaf fall occurs as a reaction to the rapidly drying soil (Worbes 1986). Measurements of litter production show the same trends as the phenological observations (Adis et al. 1979; Franken et al. 1979). Measurements in the years 1981/82 by Adis indicate a peak between May and July (high water) (see Worbes 1997), confirmed by Wittmann (1997). A second peak was measured in the dry period in November (Worbes 1997). In igapó leaf litter production shows a peak between July and August (Adis et al. 1979). Measurements indicate seasonal variation of litterfall differs between the low and high várzea

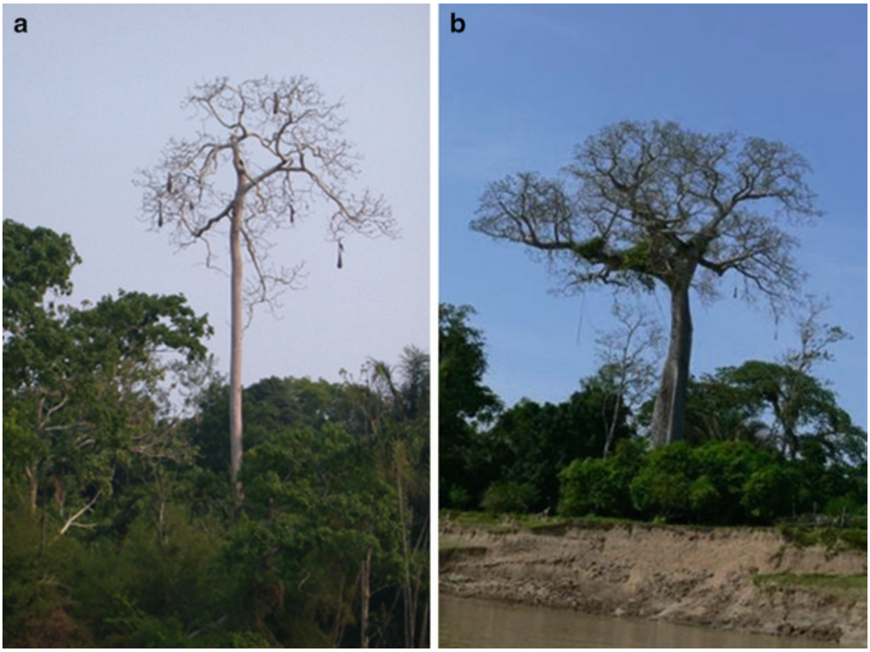

Fig. 5.4 Deciduous trees in high várzea forests during the dry season: (**a**) *Sterculia elata* (Malvaceae) (August 2005, Reserva de Desenvolvimento Sustentável Mamirauá) and (**b**) *Ceiba pentandra* (Malvaceae) (August 2006, Reserva de Desenvolvimento Sustentável Amanã) (Jochen Schöngart)

(Schöngart et al. 2010). In the low várzea litterfall peaks in April at the beginning of the aquatic phase, when rainfall reaches its maximum, while in the high várzea litterfall reaches maximum rates around November at the end of the dry season. This indicates different triggering by external factors. The low várzea responds to the flood-pulse (Schöngart et al. 2002), while most tree species in the high várzea seem to respond to seasonal variation in precipitation (Fig. 5.4).

5.4 Deciduousness Versus Evergreenness

The number of deciduous tree species in várzea and igapó is higher than in terra firme forests, which was confirmed also by Haugaasen and Peres (2005) in a direct comparison of ecosystems. This can be explained if deciduousness is advantageous at times of low tree water status: water loss of the trees is reduced by the reduction of the transpiring area through the shedding of leaves (Borchert 1991). If leaf shedding cannot be afforded, for instance because of low nutrient availability, other protections against water loss can be found, such as sclerophyllous leaves which are typical for evergreen species (Medina 1983) and are found in both várzea and igapó trees (Prance 1979; Waldhoff and Furch 2002). Due to the differences of nutrient status of the two ecosystems, it is surprising that among the documented species in igapó the strategy of deciduousness (26 species) is as common as that of leaf sclerophylly (24 species) (Parolin et al. 2002; see Table 5.2). Also, some species show deciduous behaviour in some years and evergreen in others, for example *Couepia paraensis*, *Maprounea guinanensis* (Revilla 1981; Ferreira 1991), and *Laetia corymbulosa* (Armbrüster, pers. comm.).

5.5 Flowering and Fruiting Phenology

The flood pulse acts as synchronizer for phenological rhythms in most species which is true especially for fruit maturation. Most species produce flowers at the beginning of the flooded period (Worbes 1997), and fruits reach maturity during the flooded period (Figs. 5.5 and 5.6). Moegenburg (2002) found that highest seed dispersal occurred at the highest water level.

Frankie et al. (1974) report that in Costa Rica, synchronization in flowering during particular seasons depended on climatic conditions. Nonetheless, they suggest that biotic factors, such as competition for pollinators, also may have a subtle but important influence on flowering phenology. Another study comparing two tropical dry forest sites with different annual rainfall in southern India concluded that phenological patterns depend upon precipitation (Murali and Sukumar 1994). However, they recognized the importance of ultimate causes and suggested that in some species flowering phenology might be determined by competition for pollinators (Lobo et al. 2003). Unfortunately, in Amazonian floodplains almost nothing is

Fig. 5.5 *Burdachia prismatocarpa* (Malpighiaceae) with fruiting peak at highest water levels (May 1996, Janauacá; Pia Parolin)

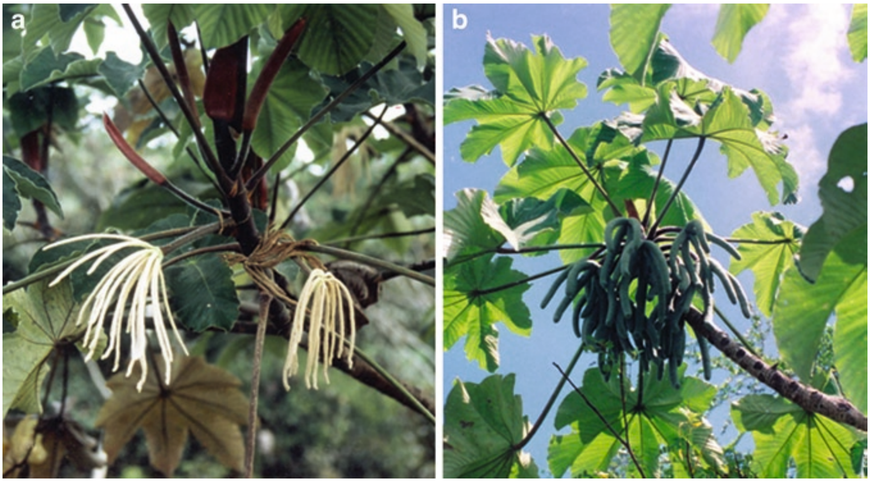

Fig. 5.6 Detail of *Cecropia* sp. (Urticaceae) with male inflorescence (**a**) and unripe fruits (**b**) (March 1995, Paraná Ariaú; Pia Parolin)

known about pollination and seasonal pollinator use of floral resources in relation to the flowering phenology of these species. It has been reported that besides the classic pollinators – bees, butterflies and birds – monkeys and bats also have an important role in the pollination (Gribel and Hay 1993, http://www.mre.gov.br/cdbrasil/itamaraty/web/ ingles/meioamb/ecossist/amazon/apresent.htm). There is an urgent need to document pollination ecology in this ecosystem.

Still, it is out of question that the timing of fruiting is important to guarantee optimization of dispersal, most species of the floodplains having hydrochoric and ichthyochoric dispersal syndromes (Ziburski 1991, Ayres 1993). The close relationship between the period of fruiting and water level is emphasized by the adaptations for floating which most fruits and seeds display in this environment (Kubitzki and Ziburski 1994; Williamson et al. 1999a,b). Some seeds are dormant as long as they are covered by water (Ziburski 1991), but many seeds lack dormancy, and a precise timing of diaspore release during inundation is important for the dispersal and germination immediately after the water retreats. The period between the floods sometimes lasts only a few weeks, and some seedlings which do not tolerate complete flooding (e.g. *Senna reticulata* in várzea, Parolin 1998, and *Aldina latifolia, Mora paraensis, Swartzia polyphylla* in igapó, Ziburski 1991), apparently depend on an efficiently timed release for establishment and survival. Fruiting in várzea occurs later than in igapó, perhaps as an adaptation to the strong sediment deposition in várzea (Ziburski 1991): this permits the colonization of freshly deposited sediments without the danger of burial, as shown for *Vitex cymosa* and *Cecropia latiloba* (Kubitzki and Ziburski 1994). On the other hand, the igapó species might be longer flooded than the várzea species, because the closed forest border in igapó establishes at mean flood heights of 9.0–9.5 m, and in the várzea already at flood levels between 7.0 and 7.5 m.

5.6 Duration and Periodicity of Phenological Events

In a study with 76 species from 30 families common in várzea or/and igapó, Parolin et al. (2002) found that the mean deciduous period was 2.3 ± 1 months (n = 11) in várzea, and 2.6 ± 1 months (n = 23) in igapó. Maximum duration of the leafless stage was 4 months in both várzea (*Crescentia amazonica, Pseudobombax munguba*, Fig. 5.7) and igapó (*Buchenavia ochnopnuma, Buchenavia suaveolens, Myrciaria dubia*; Fig. 5.8). The duration of flowering and fruiting ranged from continuous flower and fruit production during the whole year (*Salix martiana*, Oliveira 1998) to 1 month only (*Tabebuia barbata*, Parolin 1997). The longest period of flowering in várzea was 12 months (*S. martiana*, Oliveira 1998), but in igapó only 7 months (*Astrocaryum jauari*). Mean flowering duration was 3.4 ± 2 months (n = 22) in várzea, and 2.9 ± 1 months (n = 51) in igapó. Mature fruits were present for 4.9 ± 3 months (n = 41) in várzea, with a maximum of 12 months (*Luehea cymulosa, Piranhea trifoliata*, *S. martiana*). In igapó, the mean fruiting period was 3.7 ± 1 months (n = 54), with a maximum duration of 8 months (*Hevea spruceana*).

Most species have annual rhythms, but some species have supra-annual cycles. *C. pentandra* has flowers and fruits every 3 years (Gribel et al. 1999). *A. latifolia* has 2-year cycles (Ferreira, Leandro, 2009, personal communication). Other floodplain species, for example *Sloanea guianensis* in Teiú Lake várzea forest near Tefé, have supra-annual cycles of flowering and fruiting (Ayres 1993). Long-term studies are needed to detect and understand these periodicities. Some species flower at the end of the submerged period (*L. cymulosa, Pterocarpus amazonum, P. trifoliata, Macrolobium acaciifolium, Crataeva benthamii*), occasionally with a long extension into the rainy season (*Nectandra amazonum*). The fruits mature in the following flooded period. Other species start flowering in the terrestrial phase (*Albizia multiflora, Psidium acutangulum, Cordia* sp., *Annona* sp., *Calophyllum brasiliense* and

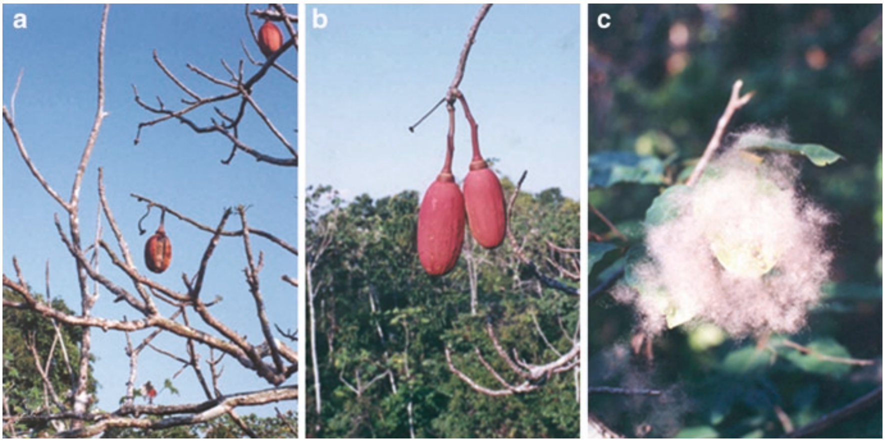

Fig. 5.7 *Pseudobombax munguba* (Malvaceae: Bombacoideae) at high water without leaves (**a**) and mature fruits (**b**) which release seeds envolved by fibres (**c**) (July 1994, Paraná Ariaú; Pia Parolin)

Fig. 5.8 *Buchenavia* sp. (Combretaceae) with newly flushed leaves at highest water levels (June 1995, Tarumã; Pia Parolin)

occasionally *Laetia corymbulosa*) and fruits mature during the aquatic phase. *Triplaris surinamensis*, a wind-dispersed species (Worbes 1986), is unique in maturing fruits only in the terrestrial phase. The majority of the tree species studied complete the whole reproductive phase of flowering and fruiting within one aquatic phase (*C. latiloba, T. barbata, Eschweilera ovalifolia, Gustavia augusta, Zygia inaequalis, Garcinia brasiliensis, Pouteria glomerata, Alchornea castaneifolia, P. munguba* and *V. cymosa*). Most fruits mature during the aquatic phase or towards the end of submersion phase with extension into the terrestrial phase. *L. corymbulosa* and *Cordia* sp. do not show a regular periodicity in flowering and fruiting (Schöngart et al. 2002).

5.7 Intra- and Interspecific Variation

Flood duration is linked to the elevation at which a tree grows along the flooding gradient (Junk 1989) and can determine the timing and duration of flowering and fruiting, as was documented for individuals of *Eschweilera parviflora* growing at different elevations in the flooding gradient (Ferreira 1998). Trees from upper elevations began to produce flowers several months later and when non-flooded (September) compared with trees from lower elevations (May–July). At the community level, in Teiú Lake várzea forest near Tefé, the fruiting peak in a high-lying community (‘restinga alta‘) was a little later than in a low-lying community (‘restinga baixa’) (Ayres 1993) which might be the result of different triggering factors (flood-pulse vs. precipitation). Other species, such as *M. acaciifolium*, did not show intraspecific differences of phenology at different elevations (Schlüter and Furch 1992).

When looking at interspecific differences, it becomes evident that there are no clear differences between várzea and igapó. Some authors state that várzea forests are mainly deciduous, while in igapó evergreen species prevail (Klinge et al. 1983; Worbes 1983, Revilla 1991). On the other hand, Parolin et al. (2002) showed that among 76 analysed species, in várzea there were even slightly more evergreen than deciduous species, and in igapó more deciduous than evergreen species. An explanation for the origin of the first statement – várzea deciduous, igapó evergreen – might be found in the timing of the deciduous period. The clear peak of deciduousness in várzea in June/July might give the observer the impression that the forest is deciduous. In igapó the period of deciduousness is less synchronized among the species and more distributed over the year, therefore a leafless period of the whole forest is not as evident.

Interspecific differences are more evident when looking at the topographical gradient within a floodplain ecosystem. In 76 analysed species (Parolin et al. 2002) species were grouped according to their occurrence at 'high' (25–28 m asl) or 'low' (21–25 m asl) elevations along the flooding gradient (Ferreira 1991; Ayres 1993). This comparison showed that the duration of the leafless period was longer at high elevations than at low elevations in the várzea, whereas in the igapó it was shorter at high elevations. In the high várzea, flowering was longer, but fruiting was shorter than at low elevations. In igapó it was the opposite: flowering was shorter at high elevations, and fruiting was longer than at low elevations. There were slightly more deciduous species at low elevations, in both várzea and igapó, whereas at high elevations there were slightly more evergreen species. This might indicate that deciduousness is an adaptation to long periods of flooding, but further data are needed to confirm this statement.

5.8 Triggers

Since long-term studies of several years are lacking, and the results presented by various authors are not directly comparable, little can be said about the triggers of phenological events. It is supposed that in the topographically low floodplains, the flood pulse (*sensu* Junk et al. 1989) is the main trigger for phenological changes and stem growth periodicity (Schöngart et al. 2002; Haugaasen and Peres 2005). The assumption that flooding triggers leaf fall is supported by a study with two identical, but temporally distinct experiments: different hydrological conditions (waterlogging, submergence and drought) were directly responsible for the changes in growth and metabolism of some species, e.g. *C. latiloba, C. benthamii, N. amazonum, S. reticulata, T. barbata*, and *V. cymosa* (Parolin 2001b). However, these experiments were performed with seedlings under semi-natural conditions.

The variety of abiotic factors such as temperature, precipitation and air humidity trigger phenological events in tropical forests (Alvim and Alvim 1978; Bullock and Solís-Magallanes 1990; Wright and Cornejo 1990; Seghieri et al. 1995). Environmental cues such as changes in water level stored by plants (Reich and Borchert 1984; Borchert 1994a,b, but see Wright and Cornejo 1990, Wright 1991), seasonal variations in rainfall (Opler et al. 1976), changes in temperature (Ashton et al. 1988; Williams-Linera 1997), photoperiod (Leopold 1951; Tallak Nilsen and

Muller 1981; van Schaik 1986; Rivera et al. 2002), irradiance (Wright and van Schaik 1994), and sporadic climatic events (Sakai et al. 1999) have been mentioned as proximate causes triggering phenological events in tropical plants. In the igapó forest of Tarumã-Mirim near Manaus, the flowering and fruiting of more than half of 29 tree species was significantly correlated with changes in the river level (Ferreira 1991), and in várzea as well (Schöngart et al. 2002). However, precipitation was also significantly correlated with the phenological events of these species, especially for evergreen species (Schöngart et al. 2002). There also might be differences between low elevations (long-term flooding) and high elevations (short-term or no flooding) indicating that different triggering factors such as precipitation (seasonal droughts) and flood-pulse act together. Some species are widespread also in non-flooded upland forests (e.g. *Ormosia excelsa, Hevea brasiliensis*, and *Triplaris weigeltiana*): their phenology is independent of flooding periodicity and is more linked to precipitation (Kubitzki and Ziburski 1994). Schöngart et al. (2002) compare the times when trees of the different phenological ecotypes such as deciduous, evergreen, semi-deciduous and stem-succulent shed and flush leaves in the floodplain forest and in the terra firme. They indicated that leaf fall, cambial dormancy and leaf flush of the evergreen, brevi-deciduous and deciduous ecotype showed a displacement of 2–3 months comparing floodplain and terra firme (Fig. 5.9). Due to the enormous catchment area of the Solimões and Negro River the water needs about 2–3 months from the headwater until it appears in the central Amazon region. This displacement in the periodicity of aquatic/terrestrial phase (floodplains) and rainy/dry season (terra firme) is reflected in the periodicity of vegetative phenology and cambial dormancy comparing the same ecotype in floodplain forest and terra firme. (Schöngart et al. 2002). This indicates that the climatic stress factors are more important than variations in day length (photoperiod).

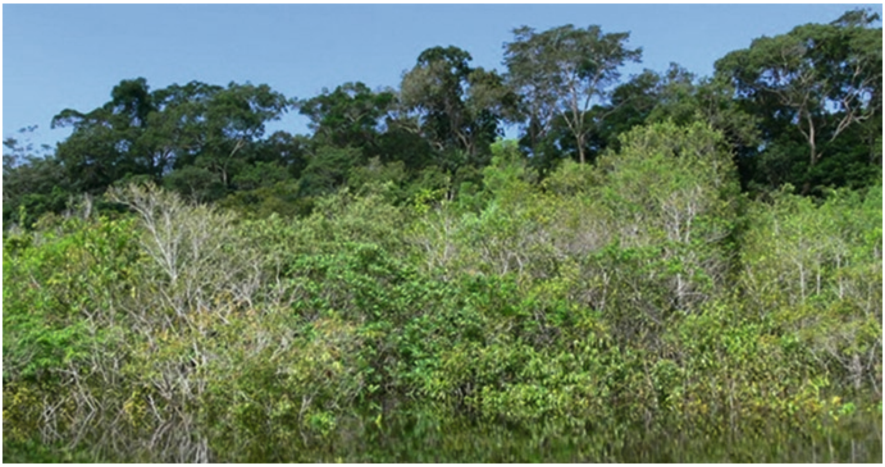

Fig. 5.9 Different phenologies in várzea (foreground) and terra firme (behind) (May 2006 at high water, Reserva de Desenvolvimento Sustentável Piagaçu-Purus; Jochen Schöngart)

The stem-succulent tree species shows a different behaviour. *P. munguba* remains without leaves until the end of the submersion phase, starting to flush in September/October until the beginning of the rainy season. Thus its dormancy period is almost synchronous with that of *Bombacopsis quinata* in the Caparo semi-deciduous forest. Borchert and Rivera (2001) relate the phenology of the stem-succulents to an endodormancy of vegetative buds controlled by the photoperiod. In our Amazonian study area the difference between the longest and the shortest day amounts about 20 min. That means a change of the daylength between consecutive days is about 6 s, however, there are indications of a higher sensitivity of stem-succulents to moderate drought stress in comparison with the other phenological ecotypes (Worbes 1999).

As mentioned earlier, flooding acted as a trigger for phenological events in *E. parviflora* growing at different elevations along the flooding gradient (Ferreira 1998), whereas Schlüter and Furch (1992) did not find intraspecific differences of phenology in *M. acaciifolium* at different elevations. The timing of flowering and fruiting in this species was independent of the beginning of the flood and its duration. Other triggers may act here, such as inherent genetic factors linked to the ecogeographical distribution and origin of the species. Some studies have suggested that plant phenology is principally constrained by phylogenetic membership or life form (Kochmer and Handel 1986; Wright and Calderón 1995). This hypothesis supports the idea that phylogenetic constraints are stronger than local selective pressure, thus members of the same taxa should have similar phenological patterns regardless of geographical location (Kochmer and Handel 1986). One example is the Malvaceae family: Lobo et al. 2003 suggest that phenological patterns of the Malvaceae family in Neotropical dry forests are mainly constrained by phylogenetic membership but also by adaptive selective pressures associated with competition for pollinators. To what extent genetically differentiated populations have differing phenologies and are specifically adapted to particular flooding conditions is not known. The plasticity of the genotypes might be tested with transplantation experiments, where seedlings from trees in upper elevations are transplanted to lower levels and vice-versa. In five *S. reticulata* trees which were transplanted to the non-flooded terra firme in Manaus, the production of flowers and fruits occurred at the same time as in individuals growing in the várzea (Parolin 1997), suggesting that precipitation and other climatical parameters are the main trigger for flowering and fruiting of this species. Leaf production, on the other hand, remained constantly high in the *S. reticulata* trees grown in terra firme which did not suffer water shortage or flooding, while at the same time in várzea, with flooding, leaf number and leaf area were strongly reduced (Parolin 1997). This indicates that in *S. reticulata* the change of water status caused by flooding is the trigger responsible for leaf shedding and production. Two identical flooding experiments with seedlings of six species from várzea, performed at different times of the year, showed that leaf phenology was linked to the flood condition, and not to precipitation or inherent cycles (Parolin 2001b). On the other hand, *M. acaciifolium* which was transplanted to terra firme was deciduous at the same time as in the várzea (Schlüter and Furch 1992) showing that for this species the trigger is not flooding. These experiments point out that different species of the floodplains react to different triggers. What the triggers are, and how they interact, is not yet understood.

In forests with a marked seasonality, changes in water availability from shifts in precipitation regimes and soil moisture have been proposed as the essential proximate and ultimate causes affecting phenological patterns (Reich and Borchert 1984). In contrast, biotic factors, such as competition for pollinators or pollinator attraction (Robertson 1895; Janzen 1967; Gentry 1974; Stiles 1975; Augspurger 1981; Appanah 1985; Murray et al. 1987; Sakai et al. 1999), competition for seed dispersers (Snow 1965), and avoidance of herbivory (Marquis 1988; Aide 1993; van Schaik et al. 1993; Coley and Barone 1996) have been interpreted as ultimate causes responsible for phenological patterns in tropical species (Lobo et al. 2003). Biotic factors have been suggested as affecting phenological synchronization between species within the same guild (Frankie et al. 1974; Stiles 1977). To which extent biotic factors are related to or even responsible for phenological events in Amazonian floodplain forests is not understood at all to date.

5.9 Conclusions

Phenology in many Amazonian floodplain trees is triggered by the periodical inundations. The position of trees in relation to inundation height and duration seems to be an important trigger particularly for the reproductive pheno-phases. However, there are inter- and intraspecific variations at all levels along the flood gradient, and also between várzea and igapó. Many Amazonian floodplain tree species occur in non-flooded ecosystems, thus phenology maybe triggered by precipitation, drought, solar irradiance, and temperature. In addition, floodplain genotypes are thought to originate from the adjacent uplands (Kubitzki 1989a). The acclimations and adaptations of trees to flooding thus were evolved in varying time scales which certainly influence life history traits and phenology of floodplain tree species.

Phenological changes reflect modifications in physiological processes associated with varying external factors. De Simone et al. (2003a,b) show for instance, that evergreen species such as *P. glomerata*, *Tabarnaemontana juruana* and *L. corymbulosa* indicated energy gain through fermentation processes and protection of the root system by the incorporation of suberin (suberinization) as a barrier of pathogens and phytotoxins. Deciduous species, such as *C. benthamii* and *V. cymosa*, on the other hand showed prevention of losses of energy reserves by down-regulated metabolism. *S. martiana* has an improved root energy status provided by an internal oxygen transport by means of aerenchyma and adventitious roots and detoxification of phototoxins by radial oxygen transport into the rhizosphere. Thus, diversity of phenological traits, such as evergreen, deciduous and brevi-deciduous ecotypes does not indicate independence of an oscillating external factor. It reflects different strategies of adaptations to prolonged flooding. Overall, our findings show that the overwhelming majority of tree species of Amazonian floodplains at low elevations respond to the flood-pulse more than to seasonal variations in precipitation. At elevations where flooding is less regular, phenological behavior seems to be triggered by precipitation, but this must be confirmed by further studies.

Chapter 6
Biochemistry of Amazonian Floodplain Trees

Maria T.F. Piedade, Cristiane S. Ferreira, Astrid de Oliveira Wittmann, Marcos Buckeridge, and Pia Parolin

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Abstract Trees colonizing Central Amazonian floodplains are subjected to extended periods of waterlogging and submersion surviving up to seven months of flooding per year. Flood is a consequence of changes in water level of ca. 10 m in the largest rivers of the region, and leads to a fast depletion of oxygen in the soil modifying the metabolism of the plants. Flooding tolerance varies between species

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and ecotypes as well as the biochemical traits and processes allowing the survival and adaptation of plant species. This results in a typical substitution of plant communities in these environments according to the depth of inundation. Amongst the developed metabolic adjustments and growth strategies and adaptations plants may show wood-ring formation, indicating annual growth reduction related to the inundation phase. The reduction of growth is preceded by stomatal closing, degradation of leaf chlorophyll, decrease of photosynthetic rates, carbohydrate translocation, and alteration of the hormonal balance. Floodplain trees develop as well protection mechanisms which can diminish damages caused by the long lasting annual hypoxia or even anoxia. Although the majority of woody plants can support periods of anoxia varying between a few hours to some days, in non-adapted species, irreversible damages can be caused leading to the death of the roots, when longer periods of flooding are imposed. These damages are attributed to the accumulation of toxic end products of the anaerobic metabolism, the loss of metabolic energy or the lack of respiration substrate. All and all the adaptations described at the biochemical level for temperate tree species inhabiting wetland are found in Amazonian floodplain trees; however, they are not enough to explain plant survival. This indicates the existence of novel mechanisms still to be found which together with the fate of the tree species inhabiting Amazonian floodplains in a changing climate are the main challenges faced by wetland scientists in the near future.

6.1 Introduction

Flooding leads to a fast depletion of oxygen in the soil and modifies the metabolism of the plants. Hypoxia, insufficient illumination under deep flooding, as well as the change in soil-chemical conditions caused by flooding (Ponnamperuma 1984) are additional stress factors for the plants inhabiting wetlands. As a result, only flood-adapted tree species occur and many of them suffer periodic growth inhibition. The reduction of growth is preceded by stomatal closing, degradation of leaf chlorophyll, reduction of photosynthetic rates, carbohydrate translocation, and alteration of hormonal balance (Schlüter et al. 1993; Kozlowski 1984a,b; Parolin et al. 2010a).

A strong pressure is imposed by flooding on the trees for the development of protection mechanisms which can diminish damages caused by the long lasting annual hypoxia or even anoxia (Ferreira et al. 2010). Flooding tolerance varies between species and ecotypes and influences species composition of plant communities along the flooding gradient. As a result a typical species zonation is observed in the areas bordering the water bodies of the Amazon floodplains (Junk 1993; Piedade et al. 2001; Wittmann et al. 2002b; Wittmann et al. 2010). Highly flood tolerant species, e.g., *Symmeria paniculata* and *Eschweilera tenuifolia* get established on the lowest sites which remain flooded for about 7 months a year. Less tolerant species, e.g. *Mora paraensis* and *Pentaclethra macroloba* are restricted to the higher parts, next to the non flooded upland (terra firme), which are flooded for shorter periods (Junk 1989; Ferreira 2000). Only few species, e.g. *Malouetia furfuracea* can colonize both high- and low-lying sites (Worbes 1997).

It is necessary to distinguish between plants which are only partly submerged, i.e. where a part of the stem and crown are still exposed to the atmosphere, and complete submergence. Species which perform well when parly submerged, do not necessarily present good performances when they are totally submerged (Parolin 2009). Typical traits of flood-tolerant plants in shallow water which are directed to amelioration of oxygen availability (Mommer and Visser 2005) are of no help in habitats with a water column of several meters. These two types of flooding require different adaptations for plant survival and growth (Parolin 2001a; Waldhoff et al. 2002; Parolin et al. 2004b).

The majority of woody plants can support periods of anoxia that vary between a few hours to some days (Gill 1970; Kozlowski 1997). In non-adapted species, irreversible damages can be observed which can lead to the death of the roots, when they are subjected to longer periods of flooding. These damages are attributed to the accumulation of toxic end products of the anaerobic metabolism, the loss of metabolic energy or the lack of respiration substrate (Drew et al. 2000).

This chapter aims at summarizing the available information on the biochemistry associated to the regulation and the adaptation processes to the prolonged periods of intense flooding in trees of central Amazonian floodplains.

6.2 Soil Alterations After Flooding

The dynamics of the water has a strong influence on soil genesis, especially in flooded ecosystems (Fiedler and Sommer 2004). Flooding of the soil promotes the adjustment of a series of physical, chemical and biological processes that have consequences for the soil quality and the growth conditions for the plants. The nature, the pattern, and the extension of the processes depend on the physical and chemical properties of the soil and on the duration of flooding.

Most Amazonian várzea soils are moderately acidic mineral soils (pH values between 4.3 and 5.3). Content of organic material is relatively low, excepting a thin organic layer at the sediment surface. About 2–3% $C_{org.}$ are found in the uppermost 10 cm mineral soil layer and a mean of about 0.7% in lower layers (Furch 2000).

At the beginning of flooding, soils become quickly anaerobic because of the fast decomposing organic material under high temperature and the slow diffusion rate of oxygen in water. Oxygen diffusion in the water is 10^4 times slower than in air (Armstrong and Drew 2002). In deep standing water, the water column near the bottom often contains H_2S and methane. The fine grained várzea soils hinder oxygenation by current even near the river channels and, at the beginning of the dry period, by diffusion from the air.

At a redox potential of about 250 mV, nitrate becomes reduced to nitrite, ammonia, and ultimately to N_2O and N_2. With decreasing redox potential at about 225 mV, manganese oxides are reduced to the soluble form of Mn^{2+} and at +100 to −100 mV, iron oxides to soluble Fe^{2+}. At –100 to –200 mV, sulfates are reduced to sulfides and

H_2S and finally below –200 mV organic material to methane (Mitsch and Gosselink 2000). Methane emission through the aerenchymatic tissue is well known from herbaceous plants (Wassmann and Martius 1997; Melack et al. 2004). To what extent trees of the Amazon floodplain forest contribute to methane transport from the sediments to the atmosphere is not known.

Periodic flooding and drought in the várzea lead to intensive processes of nitrification and denitrification in soils and water (Kern and Darwich 1997). Floodplain trees contribute by nitrogen fixation considerably to the nitrogen budget of the várzea (Kern et al. 2010). Phosphorus is often a limiting factor for plant growth in Amazonian soils. In aerobic várzea soils, part of the ortophosphate is fixed to iron and aluminum and not available to plants. Under anoxic condition, this phosphorus is transferred into a soluble form by the reduction of Fe^{3+} to Fe^{2+}. Also hydrolysis and anion exchange may release phosphate.

Trees growing in the várzea under periodically anoxic soil conditions have the advantage of a relatively good soil nutrient status (Furch 2000) that allows a quicker growth than in nutrient-poor soils of black-water floodplains (igapós) and the non-flooded upland forests. However, they have to cope with periodic anoxia and the accumulation of many potentially phytotoxic compounds, such as elevated concentrations of dissolved ionic metals that may become problematic for the root cells. Furthermore, the anaerobic microflora produces H_2S, methane, ethane, propylene, fatty acids, hydroxy- and decarbocyclic acids, unsaturated acids, aldehydes, ketones, diamines, mercaptans and heterocyclic compounds (Ponnamperuma 1984).

Barrios and Herrera (1994) suggest some of the determinants which cause seasonal differences of the efficiency in the use of nutrients by the plants in floodplain forests, in response to flooding. In a study carried out in floodplain forests of Venezuelan Amazonia, they found that the concentration of total nutrients and organic substances in the soil showed a considerable increase during the flooded period. The authors correlate this fact with soil deposition resulting from the water discharge of the riverbed. Also the slow process of decomposition and mineralization under predominantly anaerobic conditions is related to this. In this way, it is possible that the difference in soil nutrient concentrations is synchronized with the demand required for the plant, supporting the hypothesis that the flood pulse is the main driving force in this ecosystem (Junk et al. 1989).

6.3 Impacts of Soil Anaerobiosis on Plant Metabolism

The presence or absence of oxygen in the rhizosphere, determines the metabolic activity. This gas is the final electron acceptor in the oxidative phosphorylation that generates ATP. ATP is the main source of energy for the cell metabolism, and regenerates the essential NADH, the main biochemical support for the glycolysis (Dennis et al. 2000; Taiz and Zeiger 2004). With the establishment of a hypoxic environment, the aerobic metabolic pathway is deviated to an anaerobic pathway (Harborne 1988; Schlüter and Furch 1992; Ferreira et al. 2006). This pathway generates a low energetic income which is compensated by the acceleration of the glycolitic pathway (Crawford 1978). The result can be an increase of the fermentation rate, which involves the induction of key enzymes, especially alcohol dehydrogenase (ADH), pyruvate descarboxilase (PDC) and lactate dehydrogenase (LDH). Oxygen deficiency also induces the activity of other glycolytic enzymes mobilizing sucrose and starch, which are necessary for the maintenance of the energy status under anaerobiosis (Ellis et al. 1999).

The most important products of fermentation in plants are ethanol, lactate and alanine. These three metabolites are derived from pyruvate, the end product of glycolysis. They compete for substrate, but they can be produced simultaneously in plants under oxygen deficiency, in different amounts, depending on the species (Dennis et al. 2000).

In the várzea of central Amazonia, *Astrocaryum jauari* and *Himatanthus sucuuba* are examples of trees that, under the deficiency of oxygen during flooding, respond with an acceleration of glycolysis. In this case, the alcoholic fermentation becomes the standard model for energy production (Schlüter et al. 1993; Ferreira et al. 2006). The induction of activity of fermentative enzymes such as (ADH), (LDH), glutamate-pyruvate transaminoferase (GPT), and malate dehydrogenase (MDH) has been observed under anaerobic growth conditions in greenhouse experiments on seedlings of Amazonian floodplain trees as *Laetia corymbulosa*, *Tabernaemontana juruana*, *Salix martiana* and *Astrocaryum jauari* (Schlüter and Furch 1992; Schlüter et al. 1993; De Simone et al. 2002a; Haase and Rätsch 2010).

In waterlogged seedlings of *Himatanthus sucuuba*, ADH concentrations rose 15 days after the onset of hypoxic conditions and remained high throughout the 120 days of the experimental period (Ferreira 2002). This indicates that *H. sucuuba* diverts the metabolic route to the formation of ethanol as final product when subjected to anaerobiosis (Ferreira et al. 2007). In contrast, in seedlings originated from *H. sucuuba* seeds collected in non-flooded terra firme sites, ADH concentrations decreased after 30 days and seedling mortality was 100% at the end of the 120 days of the experimental period (Ferreira et al. 2010). A long-term alteration of the metabolism is observed only in species which are highly flooding tolerant. In the less flooding tolerant species, the accumulation of end products of the anaerobic metabolism can be toxic and even lethal, especially concerning ethanol (Crawford and Braendle 1996; Kozlowski 1997; Lobo and Joly 1998).

A decrease of respiration after 50 days of inundation, measured by Schlüter (1989) in the typical amazonian floodplain species *Macrolobium acaciifolium*, indicates that the anaerobic pathway of energy gain is only a provisional solution: after 200 days the concentration of ethanol increased rapidly. In *Macrolobium acaciifolium* and other species the parenchyma tissue at the ring boundaries produced in the inundation period is filled with undetermined secondary plant substances which may play a role in removal of cell poisons (Worbes 1986). To a certain extent ethanol might be directly released from the roots into the surrounding water (Kreuzwieser et al. 1999) as shown for European poplar tree species and *Salix martiana* seedlings from the Brazilian Amazon (Parolin et al. 2004; De Simone et al. 2002a,b). It may also be emitted by by the leaves into the atmosphere, as discussed later.

One of the hypotheses formulated to explain the tolerance of some plants to flooding is the "biochemical hypothesis" proposed by Crawford (1978). He suggests an alternative metabolic pathway where the intermediate products of the carbohydrate upbreak end up in organic acids such as malate instead of toxic compounds. Malate can be accumulated with less harmful consequences for the plant. The production of ethanol in this case is low and not at toxic levels (Crawford 1992; Lobo and Joly 1998). However, Crawford's hypothesis could not be biochemically proven (Harborne 1988).

In tropical trees such as *Chorisia speciosa* and *Hymenaea coubaril* (Joly and Crawford 1982) the increase in malate concentration is temporary, being observed only in the first days after the beginning of flooding. Similarly a modest increase in malate concentration was observed for *A. jauari* (Schlüter et al. 1993) and *H. sucuuba* (Ferreira 2006) in Amazonian várzeas. Due to the temporary and low amount of malate accumulated its concentration cannot be enough to support the anaerobic pathway owing to the low energetic production. However, other studies (Good and Crosby 1989; Menezes Neto 1994; Fan et al. 1997; Gaston et al. 2002) show evidences which give way to discussions about Crawford's hypothesis, suggesting that the plants possess distinct mechanisms of flooding tolerance, and that these vary depending on the species or even on the plant part involved, and more than one mechanism can prevail (Harborne 1988; Lobo and Joly 1998).

6.4 Metabolic and Hormonal Signals During Flooding

Plant hormones play a key role as mediators between environmental signals and the adaptive answers of the plants. Auxin, ethylene and giberellins are involved in these adaptive answers, initiating for example stem elongation when flooded (Voesenek et al. 1996) and the development of adventitious roots. These structures can be observed in the oxygenated water layer at the surface of the flood-water column. Hypertrophy of lenticels at the stem above the water table improve the internal oxygen status by facilitating gas entry into the stem and the roots by the shortest possible pathway (Parolin et al. 2004).

Several tree species, e.g. *Salix martiana* and *Tabernaemontana juruana*, respond to low oxygen concentrations by forming adventitious roots capable of longitudinal oxygen transport and induced by plant hormones (Haase et al. 2003; Haase and Rätsch 2010).

After flood starts, a fall in oxygen levels in the plant tissues leads to a fast inhibition of respiration. According to Visser and Voesenek (2004), the fact that a reduction of the metabolic flow occurs also with endogenous levels of oxygen indicates the existence of a signaling mechanism which is independent of the inhibition of respiration caused by modifications in the electron transport chain.

In flooding experiments focusing on the gene expression in *Arabidopsis*, Klok et al. (2002) found that the main gene classes affected were: (1) genes involved in the metabolism of ethanol; (2) genes that play a role in the process of post-injury;

(3) genes related to the ethylene metabolism, including its synthesis and signaling, and (4) genes involved in the process of programmed cell death and cell wall elongation. The first two gene classes can be considered as pre-adaptive because they afford continuity to the energy production for future flooding episodes, thus increasing the chances of plant survival. Classes 3 and 4 are related to the formation of aerenchyma, thus preparing the plant for a longer period of flooding and generating acclimation (Visser and Voesenek 2004). However, it is not clear whether classes 3 and 4 are really related to aerenchyma formation. In fact, studies with neotropical floodplain species such as *Astrocaryum jauari, Himatanthus sucuuba*, *Lithraea molleoides*, and *Genipa americana* – which are highly flooding tolerant – showed that the presence of aerenchyma in the roots was always related to a better performance of these species when subjected to flooding (Schlüter et al. 1993; Ferreira et al. 2007; Medri et al. 2007; Santiago and Paoli 2007; De Simone et al. 2002a,b; Haase and Rätsch 2010).

The role of auxins is still not clear and further studies are necessary to understand their function in the production of adventitious roots in trees of Amazonian floodplain forests. Cytokinins are probably important in this context, but only very few experiments were performed where these hormones were used or measured. Hypothetically, the death of the roots can further increase the hormonal unbalance between auxin and cytokinin in the plant under flooding because of a lack of the production of cytokinins. Theoretically, a reduction in the ratio of roots would have to induce a reduction in leaf longevity, because cytokinin seems to control the process of leaf senescence (Wingler et al. 1998).

Thus, the main mechanisms of signalling are related to the availability of oxygen, followed by a set of parallel signals which culminate in the alteration of cells in specific tissues through the activation of the process of programmed cell death. This process induces to the death of parenchyma cells forming empty spaces (aerenchyma tissues) for gas transport. There are doubts if such canals can really permeate the whole plant. However, it is known that the formation of aerenchyma is vital in Amazonian floodplain trees such as *H. sucuuba*. Seedlings of these species formed aerenchyma in the root cortex after few weeks of flooding (Ferreira et al. 2008). To what extent these structures contribute to oxygen supply in adult trees is an open question, because wood density and resistance for long distance internal gas transport of most floodplain tree species is high. Graffmann et al. (2008) suppose that pressurized gas transport significantly contributes to internal aeration of roots in Amazonian floodplain saplings growing on the higher levels in the flooding gradient, with low water columns, and is an important adaptation for establishment in these temporarily inundated habitats also in the weeks of rising and lowering water levels.

The whole subject of cellular and hormonal signalling is little understood to date. Most of the experiments were carried out with maize, rice, *Arabidopsis* and sunflower, and almost nothing is known about the enormous number of Amazonian plant species, although this is of great importance and must have a great impact on our understanding of Amazonian tree species diversity. In order to know wheter other mechanisms exist, the Amazonian floodplain forest is certainly an excellent place to be investigated.

6.5 Injuries, Free Radicals and Antioxidants

During floods, adult trees have only part of their stem flooded, but seedlings, saplings and shrubs may be completely submerged (Parolin 2009). The smaller they are, the longer is the duration of submersion, and thus the time that plants are exposed to hypoxic or anoxic conditions (Junk 1989; Parolin 1998).

Considering α-tocopherol as stress indicator (Blokhina et al. 2003, Hormaetxe et al. 2005), Oliveira Wittmann (2007b) carried out a study in greenhouse with 19 tree species of the Amazonian várzea ecosystem (Table 6.1) in order to understand whether the content of α-tocopherol was related to the topographical position of the trees on the flooding gradient. Among the studied species 42.1% are found on heights where flooding reaches a water column of 5–6 m, which corresponds to an average time of flooding of 176–231 days year^{-1}.

The initial hypothesis was that species which grow more frequently on the higher, less flooded portions in the flooding gradient have a lower α-tocopherol content than those from lower parts where flooding is more intense. However, contrary to the expectations, the results showed that the content of α-tocopherol was not related to the position of the plants in the flooding gradient (Fig. 6.1) but with their growth strategy; slow growing plants showed higher contents of α-tocopherol than fast growing species (Fig. 6.2).

Table 6.1 List of the 19 studied species, number of individuals with DBH ≥10 cm in an inventoried area of 7.25 ha in the RDS Mamirauá, and around Manaus (Wittmann 2001; Schöngart 2003). wMSDC = calculated medium level of flooding per species

Species	Total (n)	wMSDC (m)	wMSDC (days year^{-1})
Psidium acutangulum	26	6.04	231
Alchornea castaneifolia	41	5.89	228
Vitex cymosa	154	5.85	219
Tabernaemontana siphilitica	21	5.51	208
Crescentia amazonica	41	5.51	208
Macrolobium acaciifolium	13	5.44	201
Garcinia brasiliensis	10	5.2	176
Crataeva benthamii	175	5.19	186
Simaba multiflora	15	5.02	176
Pouteria glomerata	55	4.87	170
Laetia corymbulosa	151	4.84	167
Pseudobombax munguba	191	4.77	155
Zygia ampla	12	4.62	149
Nectandra amazonum	75	4.6	148
Pterocarpus amazonum	16	4.5	137
Cecropia latiloba	228	4.43	133
Annona hypoglauca	2	3.25	75
Apeiba glabra	17	2.07	41
Erythrina fusca	3	2.0	35

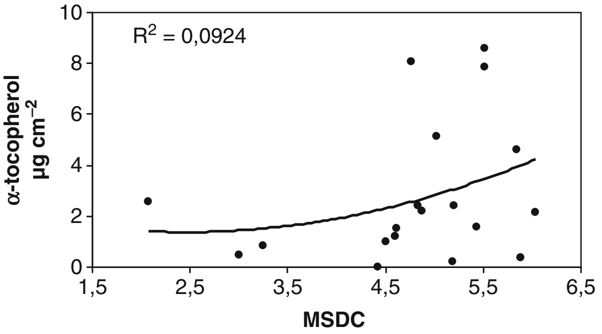

Fig. 6.1 Relation between the content of α-tocopherol in leaves and wMSDC (calculated medium level of flooding per species, in m), each point represents one of the 19 studied species

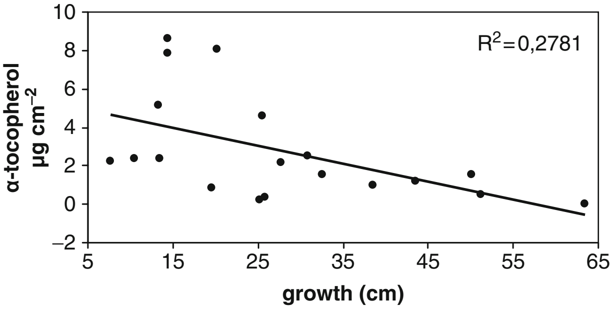

Fig. 6.2 Correlation between the content of α-tocopherol and height increment. Each point represents one of the 19 studied species ($p = 0.02$)

Since there is a relationship between the contents of α-tocopherol and the growth rhythm in Amazonian várzea tree species we may conclude that α-tocopherol plays an important role for the survival of these species in their natural environment.

6.6 Release of Volatile Organic Compounds (VOCs)

The terrestrial vegetation emits large amounts of volatile organic compounds (VOCs) to the atmosphere (Kesselmeier and Staudt 1999). VOC species such as short-chain aldehydes play an important role in atmospheric chemistry. They contribute significantly to the formation of organic aerosols. VOCs influence the oxidizing capacity of the atmosphere, generate free radicals and are involved in the production of organic nitrates (Thompson 1992; Singh et al. 1995). They also contribute to the acidity of the atmosphere by oxidation to formic and acetic acid (Talbot et al.

1990; Kotzias et al. 1997). The emission quantity and quality of VOC is under environmental and ecophysiological control.

Kreuzwieser et al. (1999, 2000) demonstrated that roots of vascular plants affected by anoxia produce high amounts of ethanol which is transported into the leaves where it can be re-metabolized by oxidation, thereby generating acetaldehyde and acetic acid as an intermediate; however, a fraction of these compounds may be lost to the atmosphere.

Acetaldehyde and ethanol may be also emitted under stress conditions such as SO_2 and O_3 exposure, water deficit, and fast changing light conditions (Kimmerer and Kozlowski 1982; Kimmerer and MacDonald 1987; Kesselmeier et al. 1997; Holzinger et al. 2000). Acetaldehyde (and formaldehyde) are exchanged bi-directionally between the vegetation and the atmosphere, i.e. they are emitted and taken up, depending on environmental and atmospheric conditions (Kesselmeier 2001). In forests of the Amazonian terra firme, both short-chain aldehydes and the corresponding organic acids were mainly taken up by the tree species, though a release was observed when ambient concentrations were below a specific compensation point (Gut et al. 2002; Rottenberger et al. 2008).

Amazonian floodplain forests are of special interest because of the potential change of emission caused by periodic root anoxia. The first results were achieved by Rottenberger (2003) and will be summarized here. Branch enclosure measurements performed in a greenhouse experiment on four different floodplain species exposed to several days of inundation showed, that emission of ethanol and acetaldehyde is inducible in response to flooding in all species. A pronounced diurnal pattern in acetaldehyde and ethanol emissions was observed with zero exchange at night, a strong emission burst in the morning, followed by a decrease in the afternoon. This pattern is interpreted to result from an ethanol accumulation in the roots at night when stomata are closed and transport is restricted by a lack of transpiration, followed by transport to the leaves driven by the light-induced transpiration stream as soon as stomata open. This general diurnal emission pattern was observed in all tree species investigated, though emission rates were substantially different among species. Maximal emission of acetaldehyde and ethanol (numbers given in brackets) differed by up to two orders of magnitude, ranging between 3 (5) nmol m^{-2} min^{-1} in *Salix martiana* and 200 (500) nmol m^{-2} min^{-1} in *Laetia corymbulosa*. Furthermore, the tree species behaved differently as far as the ratio acetaldehyde versus ethanol is concerned.

Obviously, there are large inter-specific differences not only in the ethanol production in the roots but also in the subsequent metabolic conversion inside the leaves. While *Tabernaemontana juruana* emits predominately ethanol, suggesting a limitation of leaf ADH, *Laetia corymbulosa* is a strong acetaldehyde emitter, indicative of a high ADH activity. Hence, the differences in emission rates can be related to species-specific metabolic adaptations, reflected by increased ADH activity and/or morphological adaptations of the plant to improve the oxygen availability in the roots, like formation of adventitious roots and development of aerenchyma (De Simone et al. 2002a,b; Haase and Rätsch 2010). Species with an insufficient oxygen supply need to switch over to fermentation, resulting in subsequent transport of ethanol to the leaves and emission of ethanol and its oxidation products. Species with improved oxygen supply of the roots, like *Salix martiana*, will produce no or rather low amounts of ethanol.

The different adaptive strategies are also reflected by species-specific differences in the temporal trend of the maximal emission rates over the experimental flooding period of several days. Emission rates of *Salix martiana* did not show a significant variation and remained constantly low. The other species investigated showed an increase of the maximal emission rates at first stage, indicative of increasing oxygen deficit and ethanol production in the roots, followed by a decline in emission after 3–7 days. For *Laetia corymbulosa* the decline in emission rates was associated with a progressive and pronounced reduction in leaf physiological activities (data not shown), indicating a poor acclimation to the unfavorable conditions. For *Tabernaemontana juruana* the decline in emission rates is assumed to reflect an acclimation response since leaf physiological activities (assimilation, transpiration, and stomatal conductance) were significantly less affected during the whole experimental flooding period. In this context it is also remarkable that the emission rates of fermentation products from Amazonian floodplain species were generally lower than those reported for European species (Kreuzwieser et al. 1999; Holzinger et al. 2000). This difference may indicate pre-conditioning of floodplain species towards long-lasting flooding periods.

6.7 Climate Change and Plant Responses Under Flood Stress

Carbon emissions related to the burning of fossil fuel lead to an increase of atmospheric CO_2 concentrations of our planet. Around 1930, CO_2 concentrations were 0.028% and currently we already measure 0.038%. As CO_2 is one of the main greenhouse gases, the increase of its concentration is associated to a temperature increase on the Earth surface. Increases of temperature drastically modify the amount of precipitation. Calculations and models suggest that there will be a considerable reduction of precipitation in eastern Amazonia, with an average temperature increase of 2–6°C (IPCC WGII, Fourth Assessment Report 2007). Thus, the impact of climatic changes on plants in Amazonia will be heavy, with an increase in atmospheric CO_2, increased temperatures and changes of water availability.

A fair amount of results have been produced during the last years about how plants will react to elevated CO_2. This knowledge was mainly gained from cultivated species or plants from the Northern hemisphere (see Wand et al. 1999 for a review). However, since the photosynthetic, respiratory and growth mechanisms seem to be similar in all higher plants, some extrapolations may be possible.

In general, an increase in CO_2 concentrations results in higher photosynthetic rates and a higher plant biomass accumulation. Some studies postulate an increase in wood biomass of Amazonian upland forests (Phillips et al. 2008), but growth studies in the várzea did not support this view (Schöngart et al. 2010). However, little is known on the consequences that such effect will have on the production of flowers and fruits. Studies made with soy bean, the best studied plant regarding the effects of climatic changes (Ainsworth et al. 2002), the processes of flowering and fruiting are not severely affected. While the biomass in leaves and stems declines, it increases in fruits and seeds (Long et al. 2006). This probably results from the fact that higher photosynthetic rates lead to the accumulation of additional carbon in leaves, which is used to supply the increasing energy demand of the plants reproductive process.

Some Amazonian floodplain trees have been studied with respect to their CO_2 cycles, e.g. *Hymenaea courbaril* and *Senna reticulata*. The first one is a tree of late successional stages, the second a fast-growing pioneer (Parolin et al. 2002a). In experiments with seedlings of *S. reticulata*, elevated CO_2 levels (720 ppm) led to increases in photosynthesis and biomass production (Marabesi, Aidar and Buckeridge, results not published). In *H. courbaril*, increases of photosynthesis reached 60% when seedlings were grown at CO_2 levels of 720 ppm (Aidar et al. 2002). Biomass increased by 30% and the levels of endogenous sugars (sucrose, starch and cellulose) increased in the same proportion. The availability of reserves seems to influence directly the effect of CO_2, because seedlings of *H. courbaril*, which were mobilizing their cotyledon reserves, did not show the same changes. The same was found in seedlings of other tree species of the Leguminosae family in the Atlantic Forest (Buckeridge et al. 2007). As some genera of this family which occur in the Atlantic Forest also occur in the Amazon region, some similar results can be expected.

The fact that the mobilization of reserves interacts with the general effects caused by the increase of atmospheric CO_2 levels can be important in the context of flooding, because flooded plants can be favored by the accumulation of reserves in the roots or stems (Crawford 1978). Such reserves can be used during flooding to develop adventitious roots or other structures which improve growth and survival under stress conditions. This hypothesis, however, must be proven experimentally.

Only few experiments combine elevated CO_2 concentrations and flooding. One was made with *Taxodium distichum*, a tree species of southeastern USA (Megonigal et al. 2005). The objective was to compare the answers of a microalgae with those of *T. distichum*, under the hypothesis that the microalgae would answer with growth increases and *T. distichum* would not. The hypothesis was confirmed, showing that there is a balance between the beneficial effects of CO_2 and the negative effects of flooding. Considering that *T. distichum* is highly adapted to flooding, the hypothesis of the compensatory mobilization of internal carbon reserves can be valid for several plant groups. In fact, a general mechanism can help to understand the absence of responses of plants subjected to flooding to CO_2 rises. How trees in Amazonian floodplains react is not know to date.

The predicted decrease in precipitation in certain parts of the Amazon basin will change to a certain extent the discharge pattern of Amazonian rivers. An increase of extreme droughts and floods can be assumed. Floodplain trees will adjust their position to the new hydrological conditions, moving up or down the inundation gradient, as they did it already many times during the transition between glacial and interglacial periods. Most floodplain trees can quickly react to changes of hydrological conditions, because seed dispersal by water and fishes is facilitating the occupation of new habitats. Abundance of species may change but total species number will be little affected.

6.8 Conclusions

Despite the metabolic constrains resulting of oxygen depletion in the rhizosphere and the need of leading with an anaerobic pathway very poor in energetic yield, many trees from the Amazon floodplains survive with mean annual inundation periods up to 8 months. The existing knowledge on the mechanisms and adaptations of these trees to survive in such extreme conditions of waterlogging and complete submergence in darkness is still scrappy.

The formation of aerenchyma tissues in seedlings of some Amazonian floodplain trees such as *H. sucuuba* and *Salix martiana* after a few weeks of flooding results of a sequence of signaling mechanisms in a process of programmed cell death. This ensures the long-distance O_2-transport inside the plant under conditions of flooding.

To what extent aerenchyma favors long distance transport of oxygen in adult trees is not known, although pressurized ventilation has been shown in some tree species (Graffmann et al. 2008).

Owing to the lack of studies and the high tree species diversity the current knowledge about the role of antioxidants in submerged and de-submerged tissues in Amazonian floodplain trees is scarce. The content of the antioxydant α-tocopherol appears to be related to their growth rhythm and may be of great importance on the survival of tree species beneath flooding (Oliveira Wittmann et al. 2007).

Under anaerobic conditions many tree species produce ethanol in the roots that is transported to the leaves together with its oxidation products contributing to the Volatile Organic Compounds (VOCs) emitted by the canopy. The amount of methanol and its oxidation products varies considerably between species, depending on their respiration pathways. In some species ethanol might be partially released from the roots into the rhizosphere (Rottenberger et al. 2008).

To date the adaptations to cope with flooding described for temperate tree species at the physiological, anatomical and biochemical levels are all found in Amazonian floodplain trees, however, they are not enough to explain plant survival. On the other hand, owing to the global climatic changes, alterations in the flooding regime of Amazonian rivers are expected. This may lead to a redistribution of tree species up or down the inundation gradient to occupy adequate habitats, which will be favored because of long distance seed distribution by water and fishes. Therefore, the major challenge for scientists in the near future will be to fill the gap on novel adaptations still to be found, and to predict the fate of the tree species inhabiting Amazonian floodplains in a changing climate.

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Chapter 7
The Morphology and Anatomy of Tree Roots and Their Aeration Strategies

Karen Haase and Gudrun Rätsch

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Abstract Roots of woody species of the Amazonian inundation forest demonstrate morphological and anatomic traits, which enable the trees to withstand high water levels, massive oxygen shortage in the sediment and the synthesis of harmful substances in the plant organs and in the root environment. The formation of new, mainly adventitious roots under oxygen depleted conditions and the development of porous tissues at the stem near the floodwater surface or on the basal surface of the new roots results in a short distance between the atmosphere and the active regions of the roots and facilitates the entrance of oxygen into the tree. Enhanced root porosity, generated by uniformly distributed intercellular spaces, small lacunae or aerenchyma in the root cortex, develops both constitutively and as a response to waterlogging or flooding. An interconnection of these gas spaces provides a pathway for the release of volatile harmful metabolites to the atmosphere and an internal diffusive or pressurized oxygen transport from the aboveground organs to the roots. Many tree species show a potential for root aeration under simulated flooding conditions. A moderate transport can sufficiently supply root cells if the oxygen is conserved in the root by forming a "tight" suberin barrier in the exodermis. A superior oxygen transport to the roots allows for an oxygenation of the rhizosphere by

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massive oxygen loss via a very weak suberized exodermis. Both strategies protect the roots from penetration of harmful substances into the roots – either by sealing of roots or by oxidation processes outside the roots. The experiments were carried out with saplings of a few centimetres height cultivated under greenhouse conditions. Consequently, the results only permit limited conclusions about root adaptations of adult trees in the Amazonian inundation forest.

7.1 Introduction

Water and nutrient uptake, as a primary condition for plant growth, requires that root cells maintain a high energy status. Oxygen shortage in a flooded or waterlogged soil inhibits root respiration, which normally generates chemical energy for essential biochemical processes. Alternative anaerobic glycolysis cannot fully compensate for the resulting lack of energy and, furthermore, results in the need to dispose of fermentation products; for example, the toxic compound ethanol is transported to the leaves, where it or its oxidation products are released into the atmosphere (Parolin et al. 2004b). Instead, oxygen shortage is relieved by the internal transport of atmospheric oxygen from the aboveground organs to the roots via a system of interconnected gas spaces, thus restoring aerobic conditions in root cells and improving their energy status. In addition to *Alnus glutinosa*, *Fraxinus excelsior*, *Ulmus americana*, a few *Salix* species of temperate regions, and mangroves inhabiting a variety of environments, several tropical tree species found in inundation areas are able to supply their roots and sometimes their rhizosphere with oxygen, by either an internal diffusive or pressurized gas-transport process (Andersen and Kristensen 1988; Good et al. 1992; Lobo and Joly 1998). Avoidance of anaerobiosis in the root system is an efficient mechanism that contributes to the overall adaptation of tree species to long-term flooding (Piedade et al. 2010). The role of mycorrhiza in the root system of Amazonian floodplain forests is described by Meyer et al. (2010).

This chapter provides an overview of the root morphology and anatomy of several Amazonian tree species. These were examined under simulated flooded conditions in the Max-Planck laboratory with respect to their potential for internal oxygen transport. Oxygen in the root tissue and in the rhizosphere was detected and measured using highly sensitive microelectrodes. The samples were placed in agar nutrient solution under conditions simulating anoxic flooded soil with water-filled pores (De Simone et al. 2002b). Small young seedlings or cuttings with only a few clearly fixed roots, which were subsequently harvested for anatomic examinations, were used for oxygen measurements. Among the species capable of internal oxygen transport, distinct differences were found in the nature of their gas-transport spaces, in the level of oxygenation, and in the level of oxygen starvation in their roots.

In interpreting the results, it appeared that some root types potentially able to facilitate root aeration (for instance, stilt roots) might form only in older trees. Thus, the anatomic traits detected in this study may not have been completely developed after 8–10 weeks of stagnant cultivation or at the early growth stage of the small seedlings or cuttings (Wittmann and Parolin 2005), and the internal oxygen supply of mature trees may be more effective. Nonetheless, doubts remain about the mechanism of diffusion processes in taller trees flooded up to 10 m in height (Armstrong 1979). While the responses of young trees to anoxic growth conditions in the laboratory may not necessarily correspond to those in their natural habitat, the results of the laboratory examinations at least show that there is a potential response to flooding via an internal aeration strategy.

7.2 Root Morphology and Anatomy Under Greenhouse and Simulated Flooding Conditions

Table 7.1 lists the Amazonian tree species that were successfully cultivated and examined under greenhouse conditions. The species were grown from seeds collected in the Amazonian inundation forest and cuttings were derived from the young trees that had successfully grown and developed dense root systems.

7.2.1 Roots Grown Under Oxic Conditions

Nearly all of the examined tree species developed uniformly distributed and clearly pronounced intercellular spaces in the root cortex, both in well-aerated hydroponically grown roots and in roots grown in well-drained potting soil (Fig. 7.1a,b) (De Simone et al. 2002a; Rätsch and Haase 2007; Waldhoff et al. 1998). The sole exception was *L. corymbulosa*, in which intercellular spaces in the roots were not observed (Fig. 7.1c). Additionally, small lacunae probably of lysigenous origin were present in aerobically grown roots of other species, for instance *T. pyramidalis* (Fig. 7.1d), *P. munguba* (Fig. 7.1e), *G. brasiliensis*, and *E. fusca*. Fully developed and symmetrically arranged aerenchymatous gas spaces were only observed in the roots of the pioneer species *S. martiana* (Fig. 7.1f) (De Simone et al. 2002b).

Enhanced root porosity under normoxic conditions seems to be a constitutive trait of many of the woody species inhabiting the Amazonian inundation forest and represents an anatomic basis for effective gas transport through the root tissue. Jackson and Armstrong (1999) emphasized that intercellular spaces, mainly of shizogenous origin, are a constitutive feature of many wetland species worldwide. Other authors pointed out that aerenchyma are often well developed in wetland species, even in those subjected to drained conditions (Justin and Armstrong 1987; Smirnoff and Crawford 1983). The high rate of oxygen consumption during root respiration, especially at warm temperatures, can outpace the rate of oxygen supply from the outside and so initiate the formation of aerenchyma (Drew et al. 2000).

Table 7.1 Overview of examined Amazonian tree species

Species	Family	Adventitious roots	Air spaces	Internal oxygen transport	Reference
Cecropia latiloba	Cecropiaceae	+	Pneumatophores	Not yet measured	Waldhoff et al. (1998)
Crateva benthami	Capparaceae	–	Intercellular sp.	Not yet measured	De Simone et al. (2002a)
Erythrina fusca	Fabaceae	+	Aerenchyma	+	
Garcinia brasiliensis	Clusiaceae	–	Lacunae	+	
Laetia corymbulosa	Flacourtiaceae	–	–	–	De Simone et al. (2002b)
Nectandra amazonum	Lauraceae	+	Intercellular sp.	–	Graffmann (2000); Rätsch and Haase (2007)
Pouteria glomerata	Sapotaceae	–	Intercellular sp.	–	De Simone et al. (2002a)
Pseudobombax munguba	Bombaceae	+	Aerenchyma	+	Rätsch and Haase (2007)
Salix martiana	Salicaceae	+	Aerenchyma	+	De Simone et al. (2002b, 2003)
Tabernaemontana juruana	Apocynyceae	+	Intercellular sp.	+	De Simone et al. (2002b, 2003)
Triplaris pyramidalis	Polygonaceae	–	Lacunae	+	Rätsch and Haase (2007)
Vitex cymosa	Verbenaceae	–	Intercellular sp.	Not yet measured	De Simone et al. (2002a)

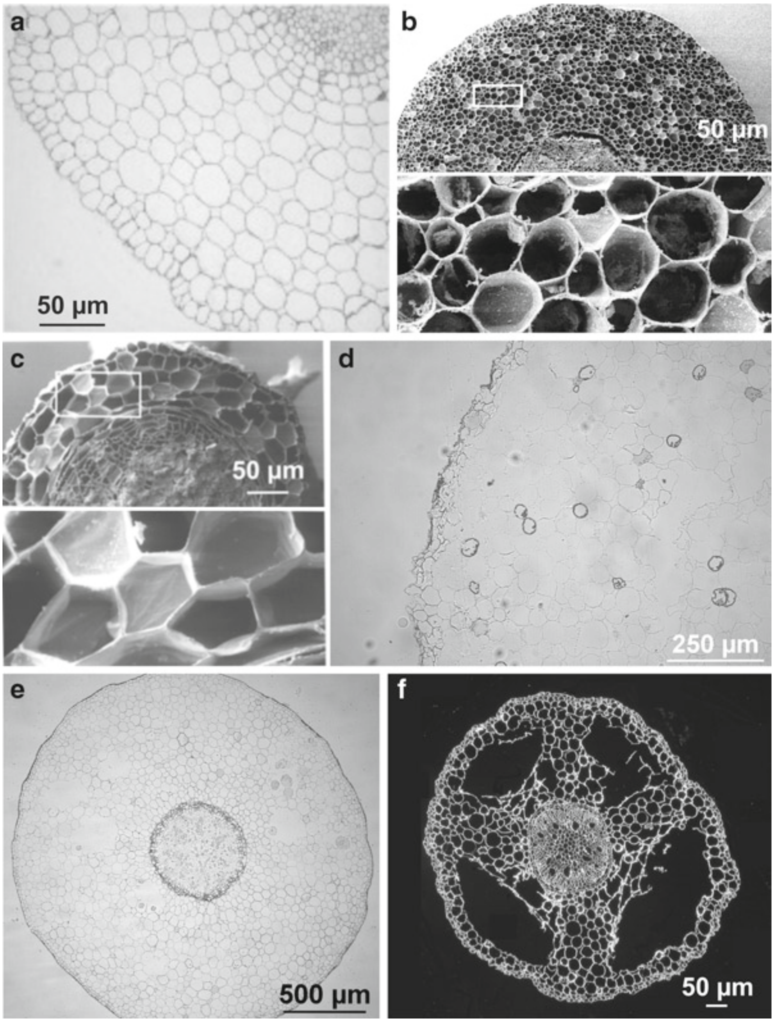

Fig. 7.1 Typical transverse sections of roots grown under well-aerated conditions. (**a**) Microtome-cut cross-section of a root of *T. juruana* stained with toluidine blue and viewed with light-field microscopy (De Simone et al. 2002a). (**b**) Scanning electron micrograph of a root segment of *P. glomerata* (De Simone et al. 2002a). (**c**) Scanning electron micrograph of a root segment of *L. corymbulosa* (De Simone et al. 2002a). (**d/e**) Microtome-cut cross-sections of a root of *T. pyramidalis* (**d**) and *P. munguba* (**e**) stained with toluidine blue and viewed with light-field microscopy. (**f**) Microtome-cut cross-section of a root of *S. martiana* stained with toluidine blue and viewed with dark-field microscopy (De Simone et al. 2002a). Cross-sections were taken 1–5 cm behind the root apices

Gas spaces in plant tissue have two main functions. On the one hand, they provide a pathway for the release of volatile harmful metabolites or gases, such as CO_2 and CH_4, to the atmosphere (Dacey 1979; Nouchi et al. 1990). On the other hand, they enable root aeration under the increasingly hypoxic conditions that follow sudden waterlogging or flooding, provided that these spaces belong to an interconnected system between the aboveground organs and the roots (Colmer 2003). It may also be the case that existing intercellular spaces and irregularly arranged small lacunae, such as found under normoxia in *T. pyramidalis, P. munguba, G. brasiliensis*, and *E. fusca*, can rapidly emerge as well developed aerenchyma in response to a lack of soil oxygen (Evans 2003; Justin and Armstrong 1987).

7.2.2 Roots Grown Under Stagnant Conditions

Flooded conditions were simulated in a greenhouse (25°C, 60–80% relative humidity) by placing pots containing young trees in potting soil in a tall basin filled with tap water, such that the water level reached 10–20 cm above the soil surface. Smaller plants (10–20 cm tall) used for oxygen measurements in the laboratory were cultivated in a climate chamber (30°C, 60–80% relative humidity) and grown in a stagnant agar nutrient solution (De Simone et al. 2002b). Wiengweera et al. (1997) discussed the advantages of agar nutrient solutions used as soil-simulating media. The transparency of the substrate and the inhibition of convectional processes therein are of great importance for microelectrode work aimed at measuring oxygen profiles in the rhizosphere. A water layer of about 2 cm above the agar surface prevented drying and shrinking of the gel. Diffusion of oxygen through the overlying water and the stagnant agar (simulating water-saturated soil) was slow. The dissolved oxygen derived from the pure nutrient solution and through direct diffusion from the atmosphere to the substrate was completely consumed in the agar medium and not measurable below the top centimeter of the agar 1 day after immersion of the tree roots in the fresh medium.

All tree species listed in Table 7.1 survived the transfer to anoxic conditions for many weeks but growth was essentially limited. Further root growth was not registered in *V. cymosa, C. benthami,* and *L. corymbulosa*, and after several days these species shed their leaves. Existing roots of *T. pyramidalis* and *P. munguba* and, to a lesser degree, of *G. brasiliensis* and *P. glomerata* grown under oxic conditions showed further elongation immediately after transfer to anoxic conditions (Table 7.2). Under greenhouse and laboratory conditions, the development of new, mainly adventitious roots was a common response to flooding in *S. martiana* (Fig. 7.2a), *E. fusca, P. munguba* (Fig. 7.2c), *N. amazonum, C. latiloba*, and *T. juruana* (Fig. 7.2b) (De Simone et al. 2002b; Graffmann 2000; Haase et al. 2003; Waldhoff et al. 1998). These roots originated randomly around the stem near the floodwater surface. In *P. munguba, E. fusca*, and *T. juruana*, roots also formed at and even below the agar surface. Initiation times were very short (2–5 days) in the pioneer species *S. martiana* and *E. fusca* as well as in *P. munguba.* In *N. amazonum, C. latiloba*, and *T. juruana*, new roots formed much later, 2–4 weeks after the start of the experiments. The diameters of all observed adventitious roots were notably larger than those of the normal roots in all species. Initially, adventitious roots grew very fast, except for those of *T. juruana* (Table 7.2), and with few extended ramifications. Fast-growing roots of *S. martiana, E. fusca*, and *P. munguba* reached a

Table 7.2 Observed growth rates of roots of different tree species immediately after transfer of the seedlings or cuttings to stagnant conditions and after initiation of new roots under stagnant conditions

		Growth rate of new roots (cm/day)	
Species	Growth rate of original roots (cm/day)	Roots originating below the agar or soil surface	Adventitious roots
C. latiloba	Not known	Not known	0.7
C. benthami	0	–	–
E. fusca	0	0.5–1	1
G. brasiliensis	<0.1	–	–
L. corymbulosa	0	–	–
N. amazonum	Not known	Not known	0.7
P. glomerata	<0.1	–	–
P. munguba	0.5	0.5	1
S. martiana	0	–	1–1.5
T. juruana	0	0.2	0.2
T. pyramidalis	0.2	–	–
V. cymosa	0	–	–

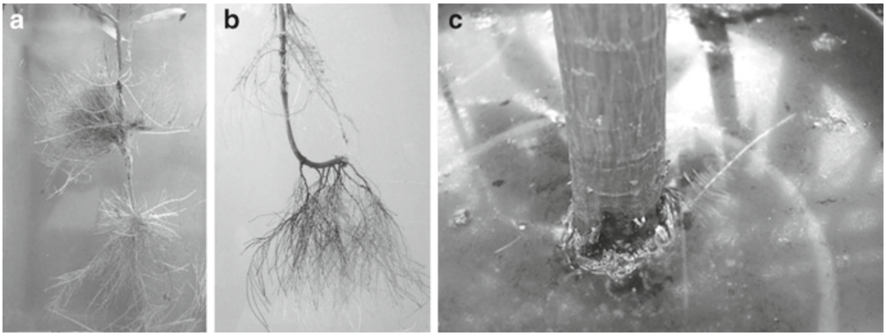

Fig. 7.2 Formation of adventitious roots in (**a**) *S. martiana* (De Simone et al. 2002a), (**b**) *T. juruana* (De Simone et al. 2002a), and (**c**) *P. munguba*

length of about 15 cm and deeply penetrated the agar medium (10–12 cm). Slow-growing adventitious roots of *T. juruana* originated above the agar surface and grew into the agar, but their lengths did not exceed 6–8 cm.

In 1998, Lobo and Joly reviewed what was known about the flood-tolerance strategies of numerous neotropical tree species. Most of the tolerant species, such as *Chorisia speciosa* (Bombacaceae) and *Talauma ovata* (Magnoliaceae), developed adventitious roots or new white and thicker roots suggesting higher porosity under waterlogging or flooding. Tree species that are commonly found along rivers and streams in temperate regions, e.g., *Salix* species, *Alnus glutinosa*, *Alnus rubra*, and *Populus trichocarpa*, also initiated adventitious roots after exposure to flooding (Armstrong 1968; Harrington 1987; Siebel et al. 1998).

7.2.2.1 The Lacunar System

The widening of existing spaces for internal gas transport and the development of a new gas-transport system (adventitious roots or roots with pneumatophore-like structure) are common responses to waterlogging and flooding not only in numerous crop species, graminaceous, and flood-tolerant herbaceous plants but also in woody species inhabiting inundation areas or coastal and riparian regions. Many scientists have intensively studied the lacunar systems of useful plants, including wheat, maize, rice, and common reed, because of the economic importance of these plants in view of damage caused by anoxic growth conditions (Allaway et al. 2001; Armstrong and Armstrong 1988; Armstrong et al. 2006; Insalud et al. 2006; Mano et al. 2006; Thomson et al. 1990). However, less is known in this context about woody species, especially those of tropical inundation areas, where oxygen consumption is particularly high because of high temperatures and high production rates. Internal aeration can occur in numerous common species via gas-transport pathways that were constitutively formed under normoxia or developed or widened in response to anoxia (Andersen and Kristensen 1988; Ashford and Allaway 1995; De Simone et al. 2002a,b; Graffmann 2000; Joly 1996; Lobo and Joly 1998; Lopez and Kursar 1999; McDonald et al. 2002; Parolin 2001a; Rätsch and Haase 2007; Waldhoff et al. 1998; Wittmann and Parolin 2005). The tropical species examined under laboratory conditions were classified according to the occurrence or development of a system of gas spaces in their roots: Group A represented species that completely lacked gas spaces (*L. corymbulosa*, Fig. 7.3a); group B consisted of species with pronounced intercellular spaces in the original roots but without further changes and lacking internal oxygen (*V. cymosa*, *C. benthami*, *N. amazonum*, *P. glomerata*, Fig. 7.3c,d); group C comprised species with intercellular spaces and small cavities in their original roots that partly extended in response to anoxia and with internal oxygen (*T pyramidalis*, *G. brasiliensis*, Fig. 7.3e,f); group D species were those capable of massive development of adventitious roots with well-developed aerenchyma and large amounts of internal oxygen therein (*E. fusca*, *P. munguba*, and *S. martiana*, Fig. 7.3g–i). The process of aerenchyma formation in the three pioneer species was described as lysigenous (De Simone et al. 2002a; Rätsch and Haase 2007). *T. juruana* (Fig. 7.3b) and *C. latiloba* belong to the latter group because of the development of adventitious roots, but in young cuttings oxygen can diffuse only through widened intercellular spaces or small cavities, similar to the mechanism in *N. amazonum* and *T. pyramidalis*. Both the developing lacunae of group C trees and the mature aerenchyma of group D species are located in the root cortex. These structures vary in their shapes and in cross-sectional area. For woody species, cross-sections from roots that developed under hypoxic or anoxic conditions and subsequently demonstrated anatomic changes compatible with the promotion of gas transport are rarely described in the literature. In a cross-section of an adventitious root of *Salix nigra*, rudimental cell walls were found between four large air spaces, similar to what has been observed in *S. martiana* and likewise indicating a lysigenous process for aerenchyma development (Kawase and Whitmoyer 1980). Mature aerenchyma randomly distributed throughout the

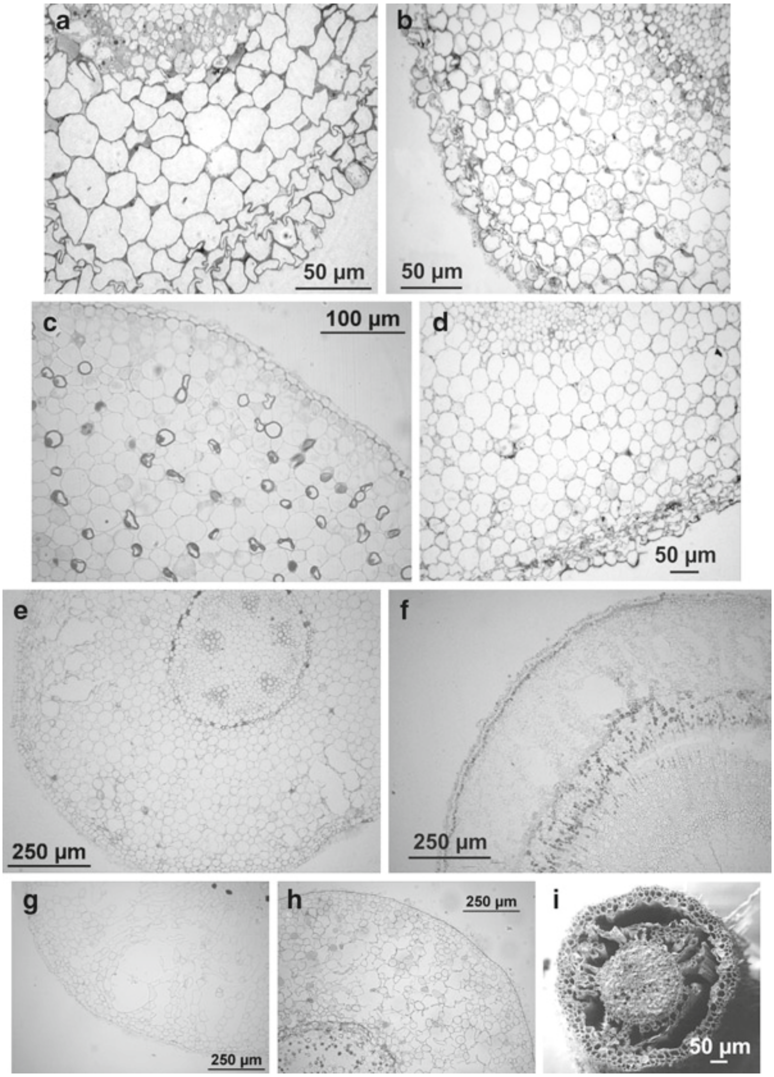

Fig. 7.3 Typical transverse sections of roots grown under anoxic conditions. Microtome-cut cross-section of roots of *L. corymbulosa* (**a**), *T. juruana* (**b**), *N. amazonum* (**c**), *P. glomerata* (**d**), *T. pyramidalis* (**e**), *G. brasiliensis* (**f**), *E. fusca* (**g**), and *P. munguba* (**h**) stained with toluidine blue and viewed with light-field microscopy. (**i**) Scanning electron micrograph of a root segment of *S. martiana*. Cross-sections were taken 1–5 cm behind the root apices

cortical parenchyma was also shown in adventitious roots of red alder seedlings (Harrington 1987). The highly flood-tolerant species *Taxodium distichum* initiates flood roots that contained large aerenchyma and pore spaces for internal oxygen diffusion (Pezeshki 1991). Anoxically grown roots of wet-site loblolly pine (*Pinus taeda*) and of pond pine (*Pinus serotina*) show enhanced aerenchyma formation compared to oxically grown roots (Topa and McLeod 1986). Highly aerenchymatous pneumatophores and cable roots of the mangrove *Avicennia marina* allow for adequate oxygen supply during the flooding period (Allaway et al. 2001).

In addition to root porosity, the permeability or porousness of the shoot-root junction is of vital importance for the aeration of flooded roots. The gas-transport rate of a tracer gas moving from the stem base to the roots was measured in small trees of five tropical species (Graffmann 2000). The author reported high transport rates for *P. munguba* and *C. benthami*, intermediate rates for *C. latiloba*, but low rates for *N. amazonum* and *V. cymosa*.

Apart from *L. corymbulosa*, all tropical tree species examined thus far develop root systems with increased porosity. This lacunar system is clearly functional and capable of development immediately after flooding. Some species, probably highly productive pioneer species, may form new, particularly porous, gas-transport systems. Further work is necessary to determine whether the adaptations to natural conditions are always anatomic or whether species also undergo physiological adaptations.

7.2.2.2 Origin of Oxygen

In tree species, lenticels located above the water surface are the points of oxygen entry into the system of gas spaces connecting the aboveground organs with the roots in anoxic environments. Several studies showed that blocking of lenticels or incubation of the base of the stem under nitrogen prevented oxygen diffusion along the internal oxygen gradient to the root apices (Andersen and Kristensen 1988; Armstrong 1968; Joly 1996; Kozlowski 1997; Lobo and Joly 1998; Topa and McLeod 1986). Specifically adapted tissues were described: hypertrophied tissue in the bark, with large intercellular spaces in the vicinity of the lenticel (Hook et al. 1970; Topa and McLeod 1986; Siebel et al. 1998); lenticels in pneumatophores of mangroves (Andersen and Kristensen 1988); lenticels on the surface of adventitious roots (Hook et al. 1970; Topa and McLeod 1986) and the permeable outer surface of vertically upwards growing young adventitious roots of *Salix cinerea* (Good et al. 1992). Adventitious roots emerge from hypertrophied lenticels in *Salix* species (Good et al. 1992) and sometimes in *Ulmus americana* (Newsome et al. 1982). They may also form in the vicinity of lenticels; for instance, in swamp tupelo (Hook et al. 1970), red alder, and black cottonwood (Harrington 1987), in wet-site pine species (Topa and McLeod 1986), and in *Ulmus americana* (Angeles et al. 1986).

Under experimental conditions, most of the examined tropical tree species developed numerous lenticels, which covered the stem surface just above the water level and also occurred below the water surface. Hypertrophied lenticels were observed in *L. corymbulosa* (Fig. 7.4a), *C. benthami*, *N. amazonum* (Fig. 7.4b), *T. pyramidalis*, *P. munguba*, *T. juruana*, and *C. latiloba* (Graffmann 2000; Haase et al. 2003; Waldhoff et al. 1998). In *T. juruana* and *C. latiloba*, adventitious roots often grew out of these structures (Haase et al. 2003; Waldhoff et al. 1998) and their origin was surrounded by hypertrophied shoot tissue (Fig. 7.4c). Additionally, in *T. juruana*, small ruptures exhibiting entry points for oxygen were found occasionally on the epidermal stem surface (Fig. 7.4d). In *S. martiana*, the porous shoot

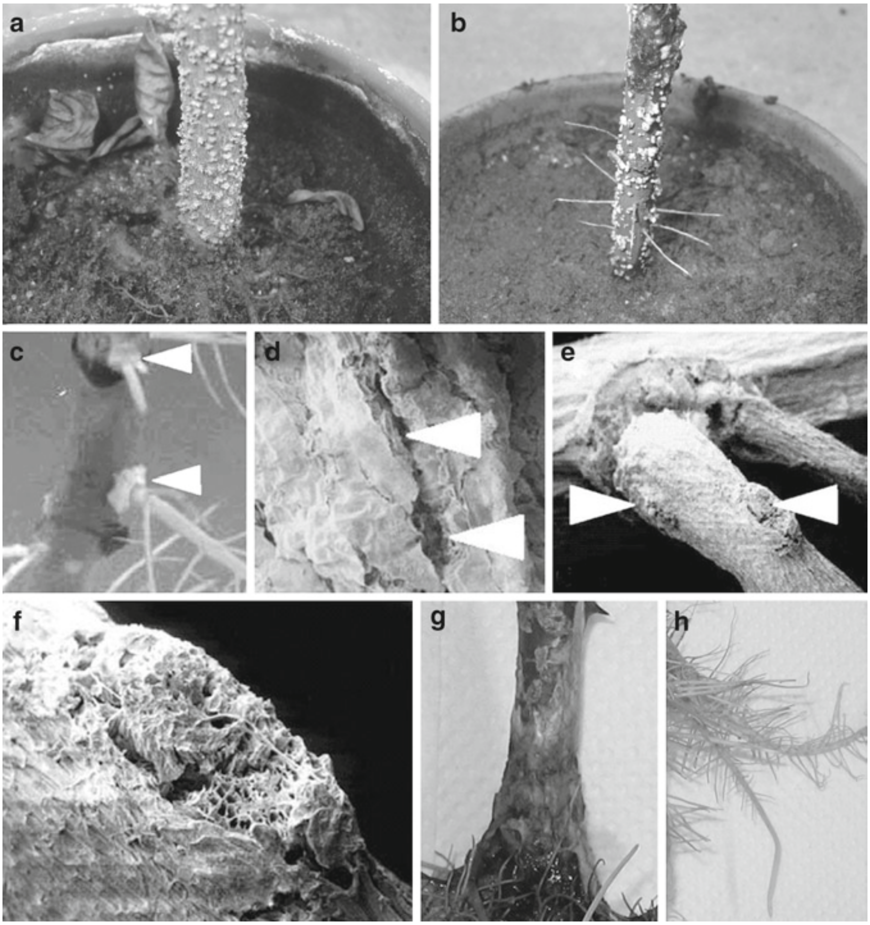

Fig. 7.4 Entry points of atmospheric oxygen. Hypertrophied stem lenticels in (**a**) *L. corymbulosa* and (**b**) *N. amazonum*. (**c**) Adventitious roots of *T. juruana* growing out of hypertrophied lenticels. (**d**) Small ruptures on the epidermal stem surface in *T. juruana*. (**e/f**) Porous shoot cortex exposed to the atmosphere around the origin of adventitious roots and protruding porous areas on the surface of adventitious roots near the basis in *S. martiana*. (**g**) Large stem ruptures revealing the highly porous shoot tissue in *E. fusca*. (**h**) Ruptures at adventitious roots in *E. fusca*

cortex connected with the aerenchymatous roots was directly exposed to the atmosphere around the origin of the numerous adventitious roots (Fig. 7.4e) (Haase et al. 2003). Areas of proliferated porous tissue were also detected at the surface of the basal portions of adventitious roots in this species (Fig. 7.4f). Since the adventitious roots of *S. martiana* often emerged up to 3 cm above the water surface, the porous areas on the roots were exposed to the atmosphere. In *E. fusca*, the highly porous shoot tissue was exposed to the air in large upright ruptures (1–2 cm long) just above the water surface (Fig. 7.4g). Vast segments of numerous newly formed roots also showed ruptures (Fig. 7.4h).

Oxygen likely enters the system of connected gas spaces directly, without a phase change or permeation through membranes. Furthermore, Haase et al. (2003) demonstrated that oxygen uptake from oxygen-rich flood waters in basal segments of adventitious roots proceeds via a highly permeable exodermis (without suberization, see below; with a phase change). In the study described here, this oxygen diffused to the more apical segments of the roots, which deeply penetrated the anoxic agar. A phase change of oxygen from oxygen-rich flood water to a gas phase may also take place in the lenticel tissue under water. This might be the reason why lenticels develop at the surface of older adventitious roots, mainly in proximity to the origin of laterals (Hook et al. 1970; Topa and McLeod 1986).

7.2.3 Oxygenation of Roots

7.2.3.1 Oxygenation Level and Root Growth

Oxygen was detected in the root cortices by means of specific electrochemical membrane microelectrodes (Unisense, Aarhus, Denmark) with tip diameters of about 20 μm. The microelectrodes were gradually driven into the root tissues in the radial direction by mechanical micromanipulators (De Simone et al. 2002b). The electrodes detect the difference in the amount of oxygen supplied by internal transport and consumed by root cell metabolism plus possible losses to the oxygen-depleted rhizosphere. Oxygen concentrations were nearly stable during penetration of the cortical tissue and decreased after penetration of the stele (Fig. 7.5). Other authors have also described and used this highly sensitive method for in vivo oxygen

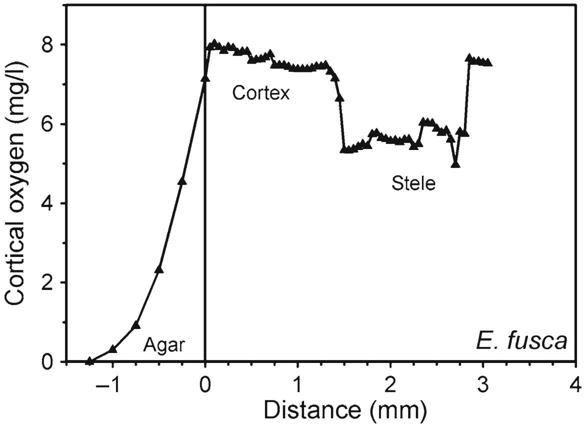

Fig. 7.5 Typical oxygen profile in the rhizosphere and root tissue of an adventitious root of *E. fusca* measured 2 cm from the root origin. The root was 4 days old and 4 cm long. The vertical axis (distance 0 mm) indicates the point of radial penetration of the microelectrode into the root

measurements in non-woody species (Armstrong 1994, Armstrong et al. 2000; Revsbech et al. 1999; Witty et al. 1987); for example, Andersen and Kristensen (1988) examined the horizontal cable roots of the mangrove *Avicennia marina* with similar electrodes.

Internally transported oxygen was detected in six of the species successfully cultivated in anoxic stagnant agar and analyzed with respect to cortical oxygen concentrations (Table 7.1). *C. latiloba*, *C. benthami*, and *V. cymosa* were not included because of difficulties in their long-term cultivation. The decreased external oxygen demand of the root system of 2- to 3-year-old trees of these three species under conditions of pressurized gas transport suggests the existence of a gas-space continuum and thus a potential for internal oxygen transport (Graffmann 2000).

Table 7.3 lists those species in which root oxygen was detected, the type of oxygenated roots, and the mean cortical oxygen concentrations. Cortical oxygen concentration at the measuring point depends on the influx, which is determined by: (a) the volume of the gas spaces and the connection between them; (b) the distances to the entry points and the lengths of the roots; and (c) the area of the free entry points. In addition, cortical oxygen concentration also depends on oxygen consumption as a function of: (d) the number of respiring root cells; (e) the number of laterals between the root origin and the measuring point; and (f) radial oxygen loss to the rhizosphere. The level of oxygenation primarily depends on the extent of the interconnected gas spaces and, consequently, on the number of respiring cells, provided that the entry points were exposed to the atmosphere and oxygen was measured at nearly the same distance to the root origin. *E. fusca*, *P. munguba*, and *S. martiana*, all of which have fully developed aerenchyma in their newly formed roots, had the highest cortical oxygen concentrations. The very young, short roots of *S. martiana* and *E. fusca* (2–3 cm long) without laterals contained 6.5–8 mg/l oxygen in the cortex 2 cm from the root origin (Fig. 7.5). This optimal oxygen supply in the vicinity of the root origin enabled deep penetration of the roots into the anoxic agar. The adventitious roots of these three species reached a length of about 15 cm under simulated flooding conditions. The numerous densely grown fine laterals emerging from older adventitious roots could also be supplied with oxygen (Fig. 7.4h). Since, under natural conditions, these three species belong to the fast-growing highly productive pioneer species, they probably rely on this

Table 7.3 Species exhibiting internal oxygen transport. Oxygen was measured in the root cortex 2–3 cm from the root origin in *E. fusca*, *G. brasiliensis*, *P. munguba*, and *T. pyramidalis*; 3–5 cm from the root origin in *S. martiana*; and 1–4.5 cm from the root origin in *T. juruana*

Species	Type of roots	Average cortical oxygen concentration (mg/l)	Reference
E. fusca	Adventitious, new	4.3	
G. brasiliensis	Original	Detectable	
P. munguba	Original, adventitious	3.4	Rätsch and Haase (2007)
S. martiana	Adventitious	3.5 ± 1.5	Haase et al. (2003)
T. juruana	Adventitious	1.3 ± 0.5	Haase et al. (2003)
T. pyramidalis	Original, new	1.5	Rätsch and Haase (2007)

avoidance strategy, which insures a high-energy status to fuel growth and development (Parolin et al. 2002c; Wittmann and Parolin 2005; Wittmann et al. 2004).

G. brasiliensis, *T. pyramidalis*, and *T. juruana* contained smaller amounts of oxygen in their cortices. The former two species had intercellular spaces and irregularly arranged still-developing lacunae in their original roots. Those less porous systems allowed only moderate oxygenation, slow root growth under anoxic conditions, shorter root lengths, and fewer laterals. Internal root aeration was able to start promptly after the sudden shift to anoxic conditions in the root environment because of the constitutively formed gas spaces. Thus, the original roots contained oxygen and likely maintained growth despite the metabolic changes in the flooded tree. Both growing original roots and the rare new roots reached maximum lengths of 5–6 cm. Oxygen measurements in the root cortex of *G. brasiliensis* were particularly difficult because the oxygen-free stele occupied almost the full cross-sectional area of the root, forming a very small cortex surrounded by a hard exodermis (Fig. 7.3f). Oxygen was only detected in the developed fine agar channel during out-tracking of the microelectrode. The detected oxygen had diffused into this channel via the electrode track through the exodermis.

A system of widened intercellular spaces in the adventitious roots of *T. juruana*, which developed after 2–4 weeks of stagnant cultivation, permitted the diffusion of atmospheric oxygen to the root apices (De Simone et al. 2002a). The relatively low porosity of these roots corresponded to their weak oxygenation. Tree species that showed only weak internal aeration under simulated flooded conditions and slowly developed the anatomic prerequisites often do not or cannot rely on this adaptation in nature. Nonetheless, our results confirmed that the potential for internal aeration is present and may be a supporting process occurring in addition to fermentation (De Simone et al. 2002b).

Cortical oxygen was not detected in the original roots of *L. corymbulosa*, *N. amazonum*, and *P. glomerata*. Internal oxygen transport was not expected in *L. corymbulosa* because of the lack of gas spaces (De Simone et al. 2002b). De Simone et al. (2002a) found only small intercellular spaces in the roots of *P. glomerata*. The transport capacity of this species is low due to either the small volume or the pattern of the intercellular spaces, which do not form a continuum. In *N. amazonum*, the presence of large intercellular spaces suggested that gas diffusion takes place in its root tissues (Rätsch and Haase 2007); however, oxygen was not detected in the original roots, perhaps because a less permeable root-shoot junction blocked internal oxygen diffusion. This suggestion is supported by an earlier study of this species (Graffmann 2000), in which a low rate of transport of the tracer gas SF_6 from the stem base to the roots was reported. Additionally, the 2- to 3-year old trees of *N. amazonum* in the study of Graffmann (2000) and those in our greenhouse cultivation (Rätsch and Haase 2007) formed porous adventitious roots potentially able to mediate gas transport. Small plants cultivated in stagnant agar nutrient solution did not form similar new roots.

Under the experimental conditions of the present study, detected cortical oxygen was derived from passive diffusion. This statement is based on the following observations: First, mass flow (thermo-osmotic pressurization) was not induced in the young plants. Second, cortical oxygen concentrations were stable for long periods

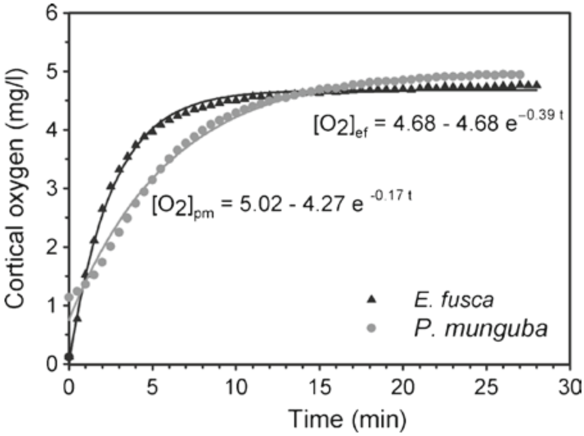

Fig. 7.6 Diffusive inflow of atmospheric oxygen into the lacunar system of adventitious roots of *E. fusca* and *P. munguba* after entry points were unsealed following the withdrawal of floodwater. Oxygen concentration was measured in the cortex 2–3 cm from the root origin. Symbols represent experimental data; lines correspond to the calculated mathematical functions, which showed simple exponential kinetics

of time (several hours, data not shown). Third, longitudinal oxygen transport showed simple exponential kinetics with constant transport rates and similar time courses in the examined species (Haase et al. 2003, Fig. 7.6). The time course of cortical oxygen was recorded after removal of the oxygen-free floodwater, which had covered the entry points of oxygen. The time needed to reestablish the cortical oxygen concentration differed in the examined species (*S. martiana*, *T. juruana*, Haase et al. 2003; *E. fusca*, and *P. munguba*, Fig. 7.6), pointing to differences in the diffusive resistances of lacunar systems.

Graffmann (2000) attempted to show the presence and importance of pressurized gas transport in five Amazonian tree species, but only *P. munguba* showed a clearly positive effect.

7.2.3.2 Sealing of Roots by Suberization

Suberization of the exodermis restricts the radial flow of water (Zimmermann et al. 2000), gases (De Simone et al. 2003c; Soukup et al. 2007), and solutes (Enstone et al. 2003) and the penetration of pathogens (Peterson 1997). Enstone et al. (2003), Hose et al. (2001), and Schreiber et al. (1999) reviewed the structure, function, and chemical composition, respectively, of those barriers and their responses to environmental conditions such as drought, flooding, salinity, redox potential of the rhizosphere, and microorganisms. Suberin is a lipophilic mixed polymer based on the fatty acids palmitic acid and stearic acid. Most wetland species contain a strong barrier to radial oxygen loss, at least in the basal zones of their roots (Armstrong et al. 2000; Colmer 2003; Končalová 1990; McDonald et al. 2002). A barrier function was demonstrated in the roots of rice (Armstrong 1971; Colmer et al. 1998, 2006), in the wetland grasses *Phragmites australis* and *Glyceria maxima* (Armstrong et al. 2000; Soukup et al. 2007), in cable roots and pneumatophores of *Avicennia marina* (Andersen and Kristensen 1988), in the sea grass *Halophila ovalis* (Connell et al. 1999), in the temperate wetland tree *Alnus glutinosa* (Dittert et al. 2006), and in other wetland species (McDonald et al. 2002). Some authors have referred to differences in the degree of restriction of outward internal root oxygen diffusion, which occurs constitutively or due to the conditions of root growth, such as nature of the substrate, external oxygenation level, and salinity, and according to root age (Colmer 2003, McDonald et al. 2002).

We demonstrated a very strong barrier to radial oxygen loss in three of the Amazonian tree species: *P. glomerata* (Fig. 7.7a, De Simone et al. 2002a), *T. juruana* (Fig. 7.7b, De Simone et al. 2003), and *T. pyramidalis* (Fig. 7.7c; Rätsch and Haase 2007). All these species exhibited similar lacunar systems that provided only small amounts of internally transported oxygen in the case of *T. juruana* and *T. pyramidalis*. Loss of oxygen due to radial diffusion would deplete this oxygen and prevent further growth. However, the strong barrier, which initiated immediately behind the root tip, conserved these small amounts of oxygen for metabolism and enabled slow elongation, up to a maximum root length of about 6–8 cm, in the young plants. The barrier existed both in original roots and in new roots formed under simulated flooded conditions (De Simone et al. 2003). A clear step in the oxygen profile at the site of penetration of the exodermis and increasing towards the root origin verified the strong restrictions to radial oxygen diffusion to the rhizosphere (Fig. 7.8).

De Simone et al. (2003) carried out quantitative chemical analysis of the suberin content of isolated peripheral cell walls in several Amazonian species to more reliably compare suberization with resistance to radial oxygen loss. The highest values corresponded to the aliphatic suberin content in *T. juruana* (3.3- to fourfold higher than those of *L. corymbulosa* and *S. martiana*). This species had a markedly tight barrier starting 2 mm from the root apex. The differences were mainly attributable to the characteristic C_{18}-unsaturated suberin markers ω-hydroxycarboxylic acid and α,ω-dicarboxylic acid.

Since internal oxygen transport was not detected in *P. glomerata*, suberization may act to impede the influx of dissolved, potentially toxic ions from oxygen-depleted soil, such as Mn^{2+}, Fe^{2+}, HS^{-}, S^{2-}, or, because of the low soil pH in Amazonia, H_2S gas molecules. Additionally the barrier could prevent the penetration of pathogens.

In *L. corymbulosa* and *N. amazonum*, which did not have an internal oxygen supply to their flooded roots, a clear but weaker extent of suberization of the exodermis was found, together with passage cells, under aerated and stagnant conditions (Fig. 7.7d, e) (De Simone et al. 2002a, 2003; Rätsch and Haase 2007). The moderate suberin incrustations could provide structural and mechanical protection against harmful particles from the anoxic rhizosphere. The high percentage of aromatics, especially of *para*-hydroxybenzoic acid, in the peripheral cell walls of *L. corymbulosa* suggested a role for suberization in pathogen defense. Similarly to salicylic acid, *para*-hydroxybenzoic acid was shown to be involved in this response (Smith-Becker et al. 1998).

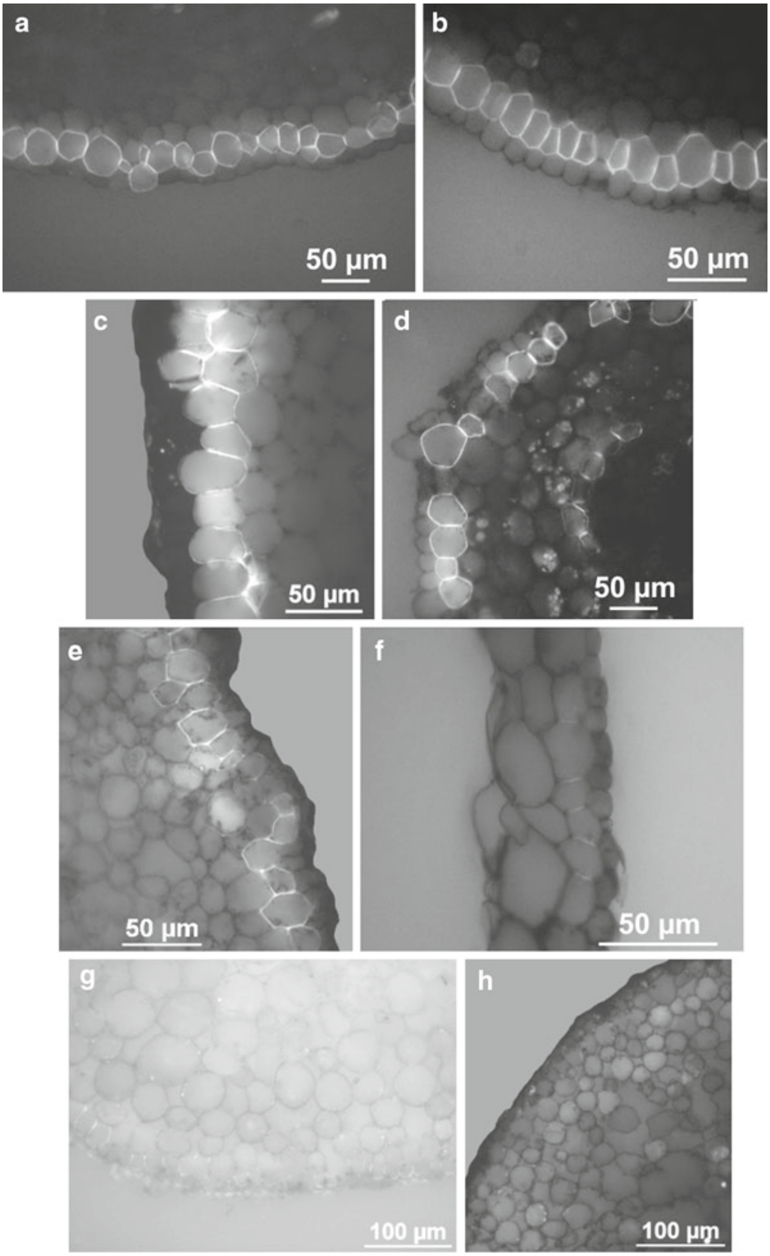

Fig. 7.7 Free-hand transverse sections of roots harvested after 10–12 weeks of anoxic cultivation. The sections were stained with toluidine blue and then neutral red and viewed with fluorescence microscopy. Specific suberin staining revealed a strongly suberized exodermis in *P. glomerata* (**a**), *T. juruana* (**b**), and *T. pyramidalis* (**c**); a moderately suberized exodermis with numerous passage cells in *L. corymbulosa* (**d**) and *N. amazonum* (**e**); and a very weak suberized exodermis in *S. martiana* (**f**) and *E. fusca* (**g**). Suberization was not detected in the root exodermis of *P. munguba* (**h**)

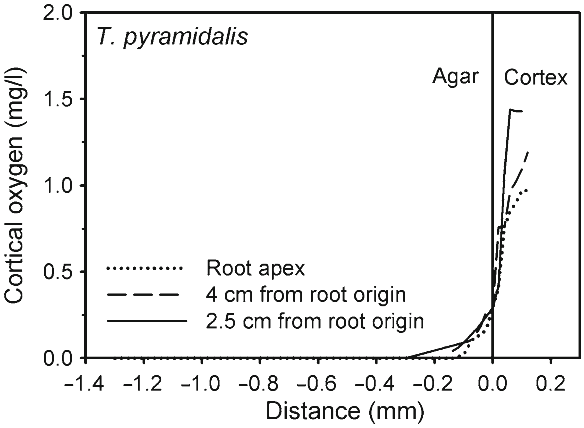

Fig. 7.8 Typical oxygen profiles in the rhizosphere, exodermis, and outer cortex at three measuring points of an original root of *T. pyramidalis*. The root was 5 cm long

7.2.3.3 Oxygenation of the Rhizosphere

Not all wetland species exhibiting internal longitudinal oxygen transport have a strong or "tight" barrier to radial oxygen diffusion to the rhizosphere (Colmer 2003). Chabbi et al. (2000) used methylene blue in agar to visualize the pattern of radial oxygen loss from well-aerated roots of *Typha domingensis* along the entire subapical region. Despite this loss, alcohol dehydrogenase activity (ADH) in the roots was low to undetectable, indicating that radial oxygen loss did not cause internal oxygen deficiencies. This highly flood-tolerant species maintained a sufficient supply of internal oxygen; thus, excess oxygen was released to the rhizosphere and created an oxidized buffer zone. A comparison of root aeration in wetland and dryland species revealed the lack of a strong barrier to radial oxygen loss not only in the dryland species but also, as the only exception in the examined wetland species, *Phalaris aquatica* (McDonald et al. 2002). A partial "barrier" to radial oxygen loss in the roots of the dicotyledonous wetland species *Rumex palustris* and *Ranunculus sceleratus* allowed for relatively consistent radial oxygen loss along the entire 8 cm of the root. The measured values did not decline towards the root apex (Visser et al. 2000). Visser et al. (2000) suggested that the ecological advantage of not forming a strong barrier to radial oxygen loss is the prolonged uptake of water and nutrients by the basal zones.

Our results support the conclusion that the combination of superior internal oxygenation and a partial "barrier" occur among wetland plants in nature (Visser et al. 2000). The roots of three of the examined Amazonian species leaked considerable amounts of oxygen along their entire lengths. The surface oxygen concentrations in adventitious roots of *S. martiana* were almost equal along the entire root, with slightly higher values at sites where laterals emerged (De Simone et al. 2002b, 2003). The constant level of the surface oxygen values despite the basipetal increase of internal cortical oxygen concentrations suggested a weak or partial "barrier", which was verified by weak suberin staining only in radial cell walls (Fig. 7.7f). Suberin content, determined quantitatively in the isolated rhizodermal cell walls, was lower in these three species than in species with a strong barrier, such as *T. juruana* (De Simone 2003). Fluorescence microscopy investigations of aerenchymatous roots of *P. munguba* and *E. fusca* grown under stagnant conditions showed also very weak (*E. fusca*) or even no (*P. munguba*) suberin incrustations in the outer cell layers (Fig. 7.7g, h) (Rätsch and Haase 2007). Oxygen measurements in the rhizosphere and in the root cortex yielded profiles verifying the lack of a strong barrier and thus massive radial oxygen losses (Fig. 7.9). The small oxygen gradient between the outer surface and the cortex, slightly increasing towards the root base, in *P. munguba* also pointed to a partial "barrier". Chemical analysis of the rhizodermal cell walls of *P. munguba* allowed detection of small amounts of suberin fragments. Oxygen gradients recorded during radial penetration of the outer cell layers of highly porous roots of *E. fusca* (Fig. 7.9) were very small or below the detection limit, while the outward diffusion of oxygen was barely restricted and thus created an oxygenated layer around the roots. *S. martiana*, *P. munguba*, and *E. fusca* feature mature aerenchyma and had considerably higher cortical oxygen concentrations than all other Amazonian species examined. Cortical oxygen concentrations between 6 and almost 8 mg/l were found 2–3 cm from the root origins, even though high amounts of oxygen diffused to the rhizosphere, numerous laterals were supplied with oxygen, and the roots grew into the agar media at a high rate, reaching a maximum length of 15–17 cm. Internal oxygen transport therefore seemed to be highly effective, so that these species were able to afford oxygen losses due to radial diffusion. *S. martiana*, *P. munguba*, and *E. fusca* are fast-growing pioneer tree species and are well-established at low sites subjected to long periods of flooding (Parolin et al. 2004b; Wittmann et al. 2004). An optimal uptake of water and nutrients, which is necessary for fast

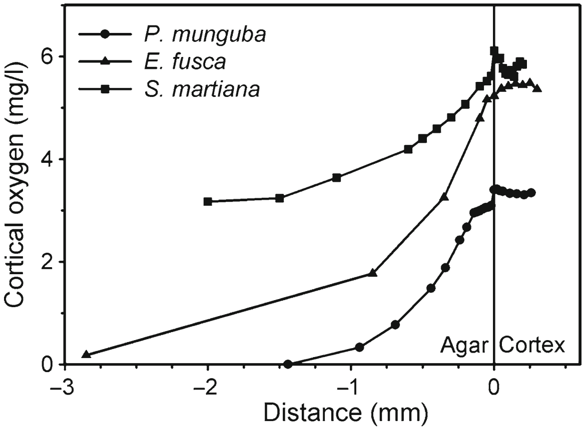

Fig. 7.9 Typical oxygen profiles in the rhizosphere, exodermis, and outer cortex of adventitious roots of *P. munguba*, *E. fusca*, and *S. martiana* measured 3 and 3.5 cm from the root origin in *P. munguba* (root length 10 cm) and *E. fusca* (root length 12 cm) and 10 cm from root origin in *S. martiana* (root length 12 cm). Massive radial oxygen loss to the rhizosphere created oxygenated zones around the roots

growth and development, may thus be realized by unimpeded radial flow from the soil to the root (Visser et al. 2000).

It is well-accepted that the barrier to radial oxygen loss, at least in the basal segments of roots, is an adaptive feature of plants to waterlogging or flooding (Colmer 2003). By restricting oxygen losses along most of their root systems, these plants are able to conserve more oxygen for growing apical meristems and for the subapical zone (Končalová 1990). Additionally, oxygen can diffuse to the rhizosphere from short laterals that emerge near the base, thereby forming an oxidized zone in this region (Colmer 2003). The broad occurrence of this spatial pattern of radial oxygen loss supports this model of root oxygenation (Armstrong et al. 2000; Colmer et al. 2006, 1998; Connell et al. 1999; McDonald et al. 2002; Soukup et al. 2007; Visser et al. 2000). Nevertheless, some species may be able to maintain high oxygen levels in their roots by effective longitudinal diffusion and a low number of respiring cells, despite radial oxygen loss (De Simone et al. 2002b; Haase et al. 2003; Rätsch and Haase 2007). Apparently, these species do not develop suberin incrustations in the exodermis to obtain a maximum root surface for nutrient uptake. In addition, they not only oxidize their own rhizosphere but also may provide oxygen for other organisms.

7.3 Conclusions

Our examinations of tree species from the Amazonian white-water floodplain forest under laboratory conditions demonstrated a potential for internal oxygen transport of different magnitudes in six of the 12 examined species. The findings suggest that most of the species with a potential for this morphologic/functional adaptation cannot rely on internal aeration during the aquatic phase in the Amazonian inundation forest, because the rapid rise and fall of the water level together with sedimentation processes inhibits the full development of essential morphologic traits (hypertrophied lenticels, adventitious roots, pneumatophores). Additionally, the large flood amplitude, up to 10 m, minimizes the importance of pneumatophores or vertically upwards growing laterals of adventitious roots and thus the effectiveness of diffusional processes therein and in the flooded tree stems. These species as well as species lacking the potential for internal aeration must benefit from adaptations ranging from the down-regulation of metabolism to sufficient energy gain for growth and development through enhanced fermentation processes. This conclusion enhances discussions regarding the detoxification of ethanol, produced during fermentation, through its upwards transport to the leaves, where it may be partly released into the atmosphere together with its oxidation products acetaldehyde and acetic acid (see Parolin et al. 2004; Parolin 2009). Wittmann and Parolin (2005) did not find pneumatophores in their study of aboveground roots in trees from a focal area of the Mamirauá Sustainable Development Reserve in western central Amazonia. However, they did remark that a notable portion of the tree species of all forest types form visible aboveground roots, which primarily serve to compensate for anoxic soil conditions under flooding. In spite of doubts concerning the activity of internal oxygen transport processes under the conditions imposed by long-term flooding at high flood amplitude, there is ample evidence supporting the establishment of this adaptation in nature. The abundance of hypertrophied lenticels occurring at a high density near the floodwater level under natural conditions is an indication of the existence and maturation of lacunar systems, which are prerequisites for effective gas transport (Graffmann 2000; Parolin et al. 2004). The ability of certain plant species to take up oxygen from the flowing and thus oxygen-rich floodwater via a non-suberized exodermis (Haase et al. 2003) shows that internal oxygen transport can take place in adventitious roots or in vertically upwards growing laterals despite an increasing floodwater level. In nature, the rapidly growing pioneer species *S. martiana* quickly (1–2 days) forms many new fast-growing adventitious roots positioned centimeters or decimeters above the water surface; the oxygen is transported only in these new roots and the distance of diffusion is always short (Haase et al. 2003; Parolin et al. 2004). Mass-flow phenomena, such as pressure-driven convective flow or Venturi-induced convective flow, have been demonstrated in trees and may enhance transport rates and transport distances in situ (Graffmann 2000; Große 1997). Since the Amazon River and its affluents represent a highly dynamic and heterogeneous river system with highly variable flooding heights, tree species with specific morphologic adaptations (for instance, pneumatophores) can become established in shallowly flooded regions. For example, the palm tree *Mauritia flexuosa* maintains root respiration via oxygen transport in numerous highly aerenchymatous pneumatophores (Granville 1974).

Field investigations similar to those of Andersen and Kristensen, who studied oxygen transport in a mangrove forest (1988), using suitable oxygen or redox electrodes could supply evidence for internally transported oxygen in central Amazonian tree species. Additionally, the results of laboratory investigations together with in situ observations clearly indicating a highly porous lacunar system (hypertrophied tissue, new thicker roots, vertically upwards growing roots) and fast growth during the aquatic phase strongly suggest the avoidance of oxygen deficiency in many central Amazonian species, including *S. martiana*, *P. munguba*, *E. fusca,* and possibly *C. latiloba*, through the maintenance of root cell respiration based on internally transported oxygen.

Chapter 8
Fine Root Systems and Mycorrhizal Associations in Two Central Amazonian Inundation Forests: Igapó and Várzea

Ulrike Meyer, Wolfgang J. Junk, and Christine Linck

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Abstract Fine root systems and mycorrhizal associations were examined in the central Amazonian várzea and igapó floodplain forests. While the várzea forest is located on fertile soil, infertile soil conditions prevail in the igapó region. Quantitative root analyses comprised of fine root length density within 8.5 cm soil depth (as a measure of root concentration) and fine root production rate within 43 cm soil depth. Fine root branching patterns and root symbioses with arbuscular/ endomycorrhiza (AM)

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or ectomycorrhiza (EM) were determined qualitatively. Fine root systems showed marked differences between the forest types. Fine root length densities, for both living and dead roots, were higher in the igapó as compared to the várzea. In spite of the greater fine root concentration within the topsoil, the fine root production rate was lower in the igapó relative to the várzea. It therefore appears that root longevity was greater and dead root decomposition lower in the igapó than in the várzea. While the majority of fine roots were concentrated within the surface horizon of the igapó, they extended to greater soil depth (43 cm) in the várzea. Root branching was characterised by higher ‘numbers of short roots’ in the igapó, while the ‘relative total root lengths’ were much higher in the várzea. In general, igapó roots were better equipped to retain nutrients within the soil-plant ecosystem through greater root concentration, greater root longevity and more intensive branching. Both forests associated predominantly with AM. EM symbiosis was only detected on Aldina latifolia in the igapó. The proposal by Singer and Araujo (1986) that the igapó forest should be viewed as an ectotrophic forest could not be confirmed by this study, as most of the tree species were symbiotically associated with the AM-type in both forests.

8.1 Introduction

The central Amazonian floodplain forests are subject to prolonged inundation periods. The várzea forest is situated in close proximity to the white-water Solimões River, whose electrolyte-rich sediment load serves as an annual nutrient input to the fertile alluvial soils (Klinge and Ohle 1964; Irion et al. 1984; Furch 1997, 2000; Furch and Junk 1997a; Junk and Piedade 2010). In contrast, sediments deposited by the electrolyte-poor, black-water Negro River contribute little to the nutrient status of the highly-weathered, infertile igapó soils (Furch 2000).

The flora and fauna of both forest types are largely controlled by the flood pulse (Junk et al. 1989). This pulse encompasses an annual alternation of an aquatic (submerged) phase and a terrestrial, temporarily dry (emerse) phase. Important in the context of forest development is that tree growth is considerably reduced in the submerged phase (Parolin et al. 2010c). Short optimal growth conditions coupled with a nutrient-poor soil environment may result in a different relative importance of nutrient cycling in the igapó as compared to the várzea forest.

Tree roots commonly form symbiotic relationships with mycorrhiza for improvement of nutrient uptake (Moyersoen et al. 2001). The two types of mycorrhizal symbioses include: ectomycorrhiza (EM) and endomycorrhiza/arbuscular mycorrhiza (AM). While EM are characterised by the formation of hyphae surrounding epidermal root cells (Hartig Net), AM are in more direct contact with roots, through penetration of host cells (Jackson and Mason 1984). Most tropical tree species associate with the AM type, which improve uptake of inorganic phosphorus (Alexander 1989). However, EM may dominate in some tropical forests, especially if they are located on infertile soils with seasonal dry periods and low nitrification rates (Janos 1983). This is in line with results of Singer and Araujo (1986), who suggested that the igapó forest should be described as an ‘ectotrophic’ forest.

The aim of this study was to examine and compare the fine root length densities, root production rates and root branching patterns of the igapó and várzea forests. Mycorrhizal associations with fine roots were investigated in both forests.

8.2 Study Area and Site Descriptions

The igapó and várzea forests are situated in central Amazonia, Brazil. The igapó forest is located adjacent to a confluent (Igarapé Nova Invéja) of the Tarumă Mirim River, which flows into the Negro River 20 km upstream of Manaus (3°S, 60°W). The várzea forest is found on the first island upriver of the confluence of the Negro River with the Solimões River (Ilha de Marchantaria) and is approximately 15 km south to the town of Manaus.

The study region is characterised by a seasonal alteration of a dry period lasting from June to November and a rainy period between December and March/May (Ribeiro and Adis 1984). A rise in water table commences approximately 4–6 weeks after the onset of the rainy season (De Simone et al. 2003a). The average annual rainfall is 2,542 mm year^{-1} (Ribeiro and Adis 1984). The average temperature range is 27.9°C in the dry period and 25.8°C during the rainy period (Junk and Furch 1985). The underlying geology of the igapó region consists of Pleistocene terraces. The várzea study area is characterised by Holocene alluvial deposits (Fittkau 1982).

Sampling was conducted in 1987 at the onset of the emerse phase. In both forest areas, three sampling plots (30 × 20 m) were selected. The plots were situated along a catena of a sloping river bank. Differences in plot elevations corresponded to variations in inundation periods. The sampling plots of the igapó forest were termed TA (2.7), TH (3.9) and TN (4.9), where numbers in brackets denote ‘months of inundation’. The várzea plots were, according to increasing inundation length/declining elevation, in the following order: MA (3.5), MB (5.4) and MH (7.1).

According to the U.S. Soil Taxonomy Classification (1990), the soil orders identified for the igapó and várzea regions were Entisols and Inceptisols, respectively. The subhorizons of the humus profiles were termed according to Babel (1971). Intergrades, e.g. Lv(FAhh), were termed by addition of the pertaining symbols, with symbols in brackets representing a lower portion of the respective components.

8.3 Materials and Methods

8.3.1 Soil Analyses and Tree Species Composition

Bulk soil samples were collected from each soil layer comprising the soil profile. Soil pH was measured in 0.02 N $CaCl_2$ after 2.5 h with a standard glass electrode. C_{total} (C_t) was determined by the potassium dichromate oxidation procedure (Schlichting et al. 1995). N_{total} (N_t) was analysed by the Kjedahl method (Schlichting et al. 1995). P_{total} (P_t) and K_{total} (K_t) were extracted from soil with 30% HCl. P_t was measured spectrophotometrically after the addition of molybdate-vanadate solution at a wavelength of 440 nm. Caesium-aluminium buffer was added to the extract for determination of K_t by AAS.

Tree species composition was recorded for each sampling plot using trees >5 cm stem diameter at breast height. Epiphytes were not accounted for in this study.

8.3.2 Root Analyses

Investigation of the fine root systems included: root length density within 8.5 cm soil depth; root production within 43 cm soil depth; root branching patterns and mycorrhizal associations. While root length density and root production investigation involved quantitative analyses, root branching patterns and mycorrhizal associations were examined qualitatively.

8.3.2.1 Fine Root Length Density

Fine root length (per soil area) and fine root length density (per soil volume) were examined on soil blocks with polished vertical surfaces (preparations after soil impregnation with polyester resin, Babel 1979). An advantage of this method is that roots can be assigned exactly to the individual layers of the humus profile, which sometimes are merely a few millimetres thick. The values obtained by this method are higher than those derived from washing and sieving methods. This is true for living roots and still more pronounced for dead roots as no losses occur by breaking off parts of the root systems.

The number of section profiles of fine roots (<1 mm) (Q) per test area (A) was counted under a stereomicroscope with magnification 25×. At least six test squares (5 × 5 mm) were placed at random in each subhorizon of each of 5 blocks (60 × 120 mm) per sampling date. The root length densities J_v (cm cm^{-3}) were calculated as follows (Weibel 1979):

$$J_v = 2\,Q / A$$

The factor 2, which is only valid for isotrophism, was found to be a sufficiently good approximation in this study.

Fine root length (cm cm^{-2}) was calculated by multiplication of J_v with the soil horizon thickness.

The fine roots were classified into two categories:

- Living roots – rhizodermis turgescent or slightly shrunken, cortex parenchyma and central cylinder bright to slightly brownish.
- Dead roots – cortex and central cylinder dark, or cortex milky, no central cylinder, exodermis wrinkled.

8.3.2.2 Fine Root Production

The vertical distribution of newly developed fine roots and their production rates were examined in situ in the medium-elevated plots of the igapó (TH) and várzea (MB) forests over time. Six glass tubes (43 cm length), containing a mini-rhizotron (Wolf GmbH, Knittlingen) each, were vertically inserted into soil per plot. Adequately sized holes were drilled beforehand to ensure close contact between the glass tubes and the surrounding soils. One month after installation, a camera (Olympus OM 4) was attached to the mini-rhizotron to scan the surfaces of the glass tubes at certain depth intervals. The numbers of newly developed fine roots were counted per 1 cm soil depth using a surface area of 4 cm^2. This procedure was repeated five times on a monthly basis.

The fine root production rate was calculated from the sum of the positive differences of the fine root numbers between the six dates (Hansen and Steen 1984; Vogt et al. 1986). The production rate was expressed as root length density (cm cm^{-3}), assuming that a fine root touching the surface of the mini-rhizotron tube can be handled like a root section profile in a soil section plane.

8.3.2.3 Fine Root Branching Pattern

Investigation of fine root branching patterns was only feasible for trees exhibiting highly branched root systems within close distance to the stem and the soil surface. Trees with long tap roots were not included in this study.

The whole root system, from the stem to the final branches, was uncovered. Root first order end sections (25 cm) with all their branches (including third/last order branching) were removed. The roots were conserved with AFE-solution. The fine root branching systems were later analysed with the aid of a semi-automatic image analyser (MOP-MO2, Kontron). The analyser calculated mean values of the lengths and numbers of root segments. Schematic drawings were produced from the values obtained according to the method of Kottke (1986) taking 10 cm root first order as the reference length (Fig. 8.1). In addition, the following ratios were calculated for numerical characterisation of the branching types:

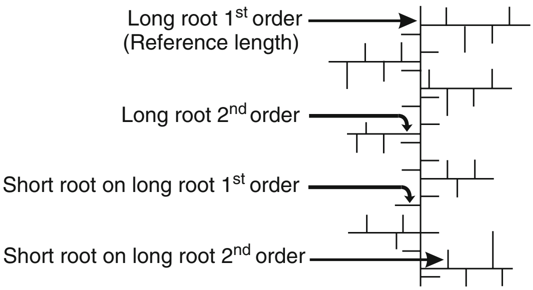


Fig. 8.1 Terminology of root segments

- Relative number of short roots (cm^{-1}): number of short roots on long roots first and second order per centimeter of long roots first and second order.
- Relative total root length: length of all long and short roots (cm) per cm of long roots first order.

8.3.3 *Mycorrhizal Association*

Mycorrhizal association types with fine roots were examined using the AFE-conserved root samples. The root sections were stained with Trypan blue in lactophenol (Phillips and Hayman 1970) and examined microscopically (40×–100×) for intracellular hyphae and possibly vesicles (AM). EM associations were examined microscopically by the use of permanent slides containing non-dyed root segments embedded in glycerine.

8.4 Results

8.4.1 *Soil Chemical Parameters and Tree Species Composition*

Table 8.1 depicts the chemical parameters corresponding to the soil layers of the igapó and várzea soil profiles. In general, organic matter accumulation, as indicated by C_t contents, was greater in the topsoils of the igapó relative to the várzea forest. C_t increased in both forests with increasing inundation lengths. Similarly, N_t was usually higher in the topsoils of the igapó plots. In contrast, P_t and K_t concentrations were, at each soil depth interval, higher in the várzea than in the respective igapó plots. In both forests, nutrient concentrations (C_t, N_t, P_t, K_t) declined with increasing soil depth.

The várzea and igapó forests were heterogeneous in terms of tree species composition and numbers of individual species (Table 8.2). In this study, a total of 67 tree species were detected in the investigated igapó plots and 31 species were identified in the plots of the várzea forest. Three species were common to both forests. Both forests showed a distinct zoning of tree species composition according to plot location along the catena (Table 8.2).

A greater above-ground biomass production was observed in the várzea as compared to the igapó forest. Trees rarely exceeded a stem diameter of 15 cm in the igapó forest, while thicker trees were often noticed in the várzea plots (data not shown).

8.4.2 *Fine Root Length Density*

Fine root length densities (cm cm^{-3}), for both living and dead roots, were significantly higher in the igapó as compared to the várzea topsoils (analysis of

Table 8.1 Chemical soil characteristics according to plot location in the igapó and várzea forests

Forest type	Plot	Soil horizon	Horizon thickness (cm)	pH ($CaCl_2$)	C_t (%)	N_t (%)	C/N	P_t (ppm)	K_t (%)
Igapó	TA	L	2	4.0	50.7	1.60	32	334	0.13
		Ahh	3	3.5	7.0	0.40	18	223	0.05
		(Ah)Gr	15	3.8	0.8	0.06	13	62	0.02
		G(o)r	30	4.3	1.0	0.05	22	90	0.02
		GoBv	52	4.1	0.5	0.04	14	82	0.03
	TH	L	2	3.7	49.0	1.10	45	242	0.09
		(F)Ahh	4	3.4	11.5	0.60	19	239	0.11
		(Ah)Gr	10	3.7	2.5	0.20	16	86	0.09
		G(o)r	10	3.7	0.9	0.10	9	76	0.09
		Go	76	3.8	0.8	0.07	11	99	0.12
	TN	L	1	4.3	51.9	1.00	52	234	0.39
		F(Ahh)	2	3.4	35.6	1.60	22	546	0.26
		(F)Ahh	2	3.5	16.9	0.90	19	400	0.21
		Ah(Gr)	3	3.6	6.2	0.50	12	219	0.14
		(Ah)Gr	11	3.7	2.2	0.20	11	109	0.12
		G(o)r	17	3.7	1.2	0.09	14	82	0.13
		Gro	65	3.8	0.6	0.05	13	170	0.11
Várzea	MA	L	1	5.1	41.5	1.50	28	921	0.36
		Ahh	4	4.2	6.2	0.40	16	561	0.78
		(Ah)Gor	5	4.2	1.2	0.10	12	255	0.77
		Gro	14	4.2	0.9	0.09	10	286	0.77
		II BvGo	44	5.3	0.2	0.02	10	439	0.28
		Gro	33	5.8	0.5	0.04	13	516	0.41
	MB	L	1.5	4.6	44.3	1.30	34	812	0.27
		Fahh	1	4.0	18.7	1.30	15	800	0.60
		Ahh	3	3.9	4.2	0.30	14	495	0.71
		Gro	6	4.1	0.8	0.10	8	231	0.79
		Go	25.5	4.5	0.5	0.10	5	336	0.64
		II BvGo	64.5	5.3	0.2	0.02	10	448	0.25
	MH	L	2	5.0	43.9	1.60	27	1,210	0.89
		Fahh	1.5	4.0	22.0	1.30	17	797	0.67
		Ahh	3	4.1	4.4	0.30	15	509	0.91
		Gro	7	4.2	1.0	0.10	10	251	0.82
		Go	35	5.1	0.8	0.07	11	393	0.96
		II Gro	46.5	6.1	0.6	0.05	12	545	0.61

variance, 5% Confidence Interval (C.I.) (Fig. 8.2). Specifically, the fine root lengths (cm cm^{-2}) of living roots were 1.8–4.8 times greater in the igapó than in the respective várzea plots. Root lengths determined for dead roots were 1.3–3.0 times higher in the igapó relative to the várzea plots. For both forests, highest root length densities were associated with the humus-rich loose Ahh horizons, which were mixed with organic materials from the humus cover by animal perturbation.

Table 8.2 Description of vegetation in the igapó and várzea[a]

Forest type	Plot location and size	Number of tree species	Number of individuals	Diversity (Shannon-Weaver)
Igapó	TA (600 m^2)	29	85	3.09
	TH (600 m^2)	33	73	3.25
	TN (600 m^2)	36	119	2.97
	TA+TH+TN (1,800 m^2)	67	277	3.81
Várzea	MA (600 m^2)	15	64	2.34
	MB (600 m^2)	16	35	2.35
	MH (600 m^2)	14	65	2.01
	MA + MB + MH (1,800 m^2)	31	164	2.93

[a] Species names in Meyer (1991)

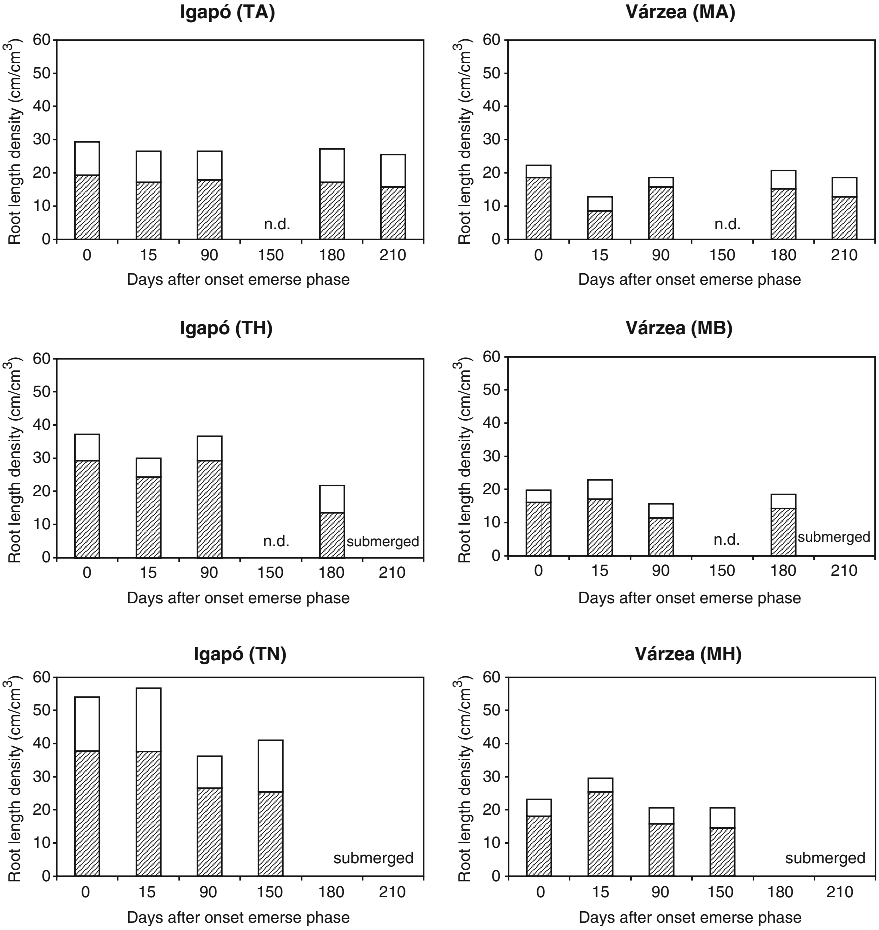


Fig. 8.2 Root length densities of dead (striped bars) and living roots (white bars) within 8.5 cm soil depth in the Igapó and Várzea plots (n = 5); n.d. = not determined

Differences in root length densities were negligible for the shortest inundated plots of both forests (TA. MA) (Fig. 8.2). An increase in the amount of fine roots with increasing inundation length was prominent in the igapó, but less pronounced for the várzea forest. In particular, fine root lengths determined for the igapó forest were 35% higher for living and 45% higher for dead roots in the longest inundated TN plot relative to the shortest inundated TA plot.

Minor fluctuations in root length densities were observed for both dead and alive roots in all plots during the emerse phase (Fig. 8.2). Thus, the proportion of living roots remained relatively constant in both forests between the beginning and end of the emerse phase.

8.4.3 Fine Root Production

Depth distribution of newly-formed fine roots and their production rates were only examined in the medium-elevated plots of the igapó (TH) and várzea (MB) forests. Comparison of both plots revealed marked differences in the vertical distribution of fine roots. With respect to the igapó forest, the maximum concentration of young fine roots was found within 0–16 cm soil depth (Fig. 8.3). This rooting depth coincided with the extent of the AhGr horizon. Below, a humus-free mineral horizon was located, which contained noticeably fewer roots (16–25 cm depth). Only few roots were occasionally detected up to 43 cm soil depth. In contrast, two peaks in fine root concentrations were identified in the soil profile of the várzea forest (Fig. 8.3). The first peak corresponded to the Ahh/AhGOR horizon within 4–8 cm soil depth. Fine root development was then sparse between 12 and 38 cm soil depth. The second peak and highest concentration of fine roots was observed within 38–43 cm of the várzea soil profile.

The production rates of new fine roots were, for the soil depth intervals 0–8 cm and 33–43 cm, significantly higher in the várzea than in the igapó plot (T-test, 5% CI) (Fig. 8.4). With respect to the latter depth interval, the fine root production rate determined for the igapó plot accounted only for 6% of the one identified in the várzea. Similar production rates were, however, determined for both plots between 8 and 32 cm soil depth.

8.4.4 Fine Root Branching Pattern

Fine root branching patterns were investigated using 43 and 29 tree species of the igapó and várzea forests, respectively. For each species, one individual tree was examined in order to gain a more complete overview of the different root branching types, rather than investigating fewer tree species more intensely. Both forests showed distinct differences in root branching types. Figures 8.5 and 8.6 illustrate

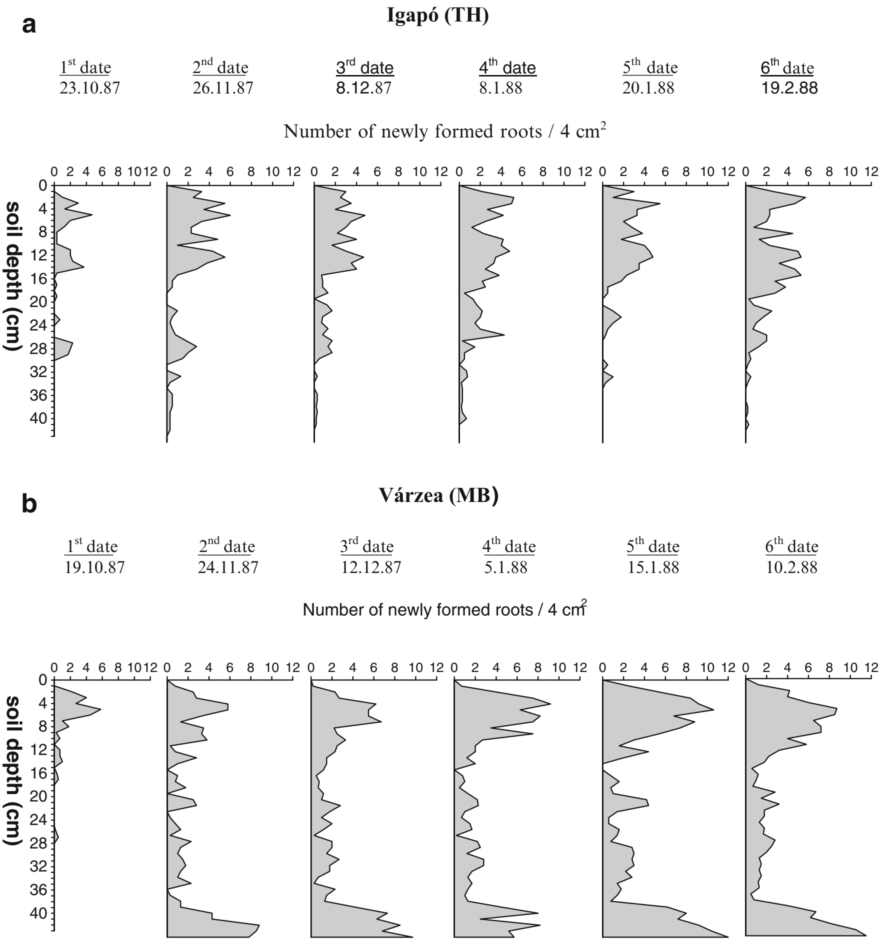


Fig. 8.3 Depth distributions of fine roots at different times during the emerse phase in the igapó (**a**) and várzea (**b**)

examples of root branching patterns identified for tree species in the igapó and várzea forests, respectively. The 'relative numbers of short roots' were considerably higher in the igapó than in the várzea plots. While many of the igapó tree species produced exceptionally high 'relative numbers of short roots' (up to 19 short roots cm^{-1}) in the different plots, none of such extreme root branching patterns were established by várzea tree species. In contrast, the 'relative total root lengths' were significantly higher in the várzea forest. Typical of the igapó forest was the species *Cynometra spruceana* (Fig. 8.5), while *Labatia glomerata* was prevalent in the várzea (Fig. 8.6).

Variations in inundation periods did generally not impact on root branching types in both forests. The tree species *Triplaris surinamensis*, which was explicitly

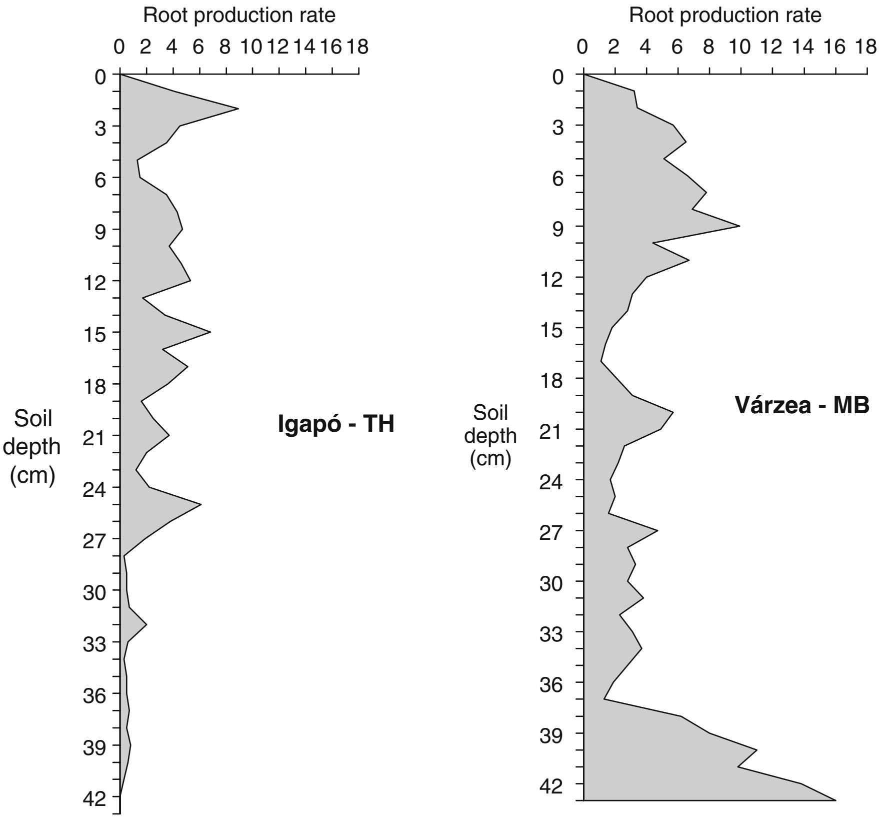
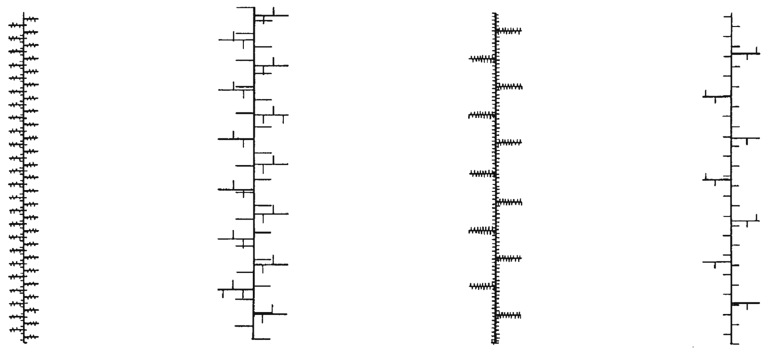


Fig. 8.4 Fine root production rates (number of newly formed roots/4 cm^2/5 months) during the emerse phase in the plots TH (igapó) and MB (várzea)

examined using two individual trees at different plot locations in the várzea forest (MA and MB), developed a fairly constant geometry of its root system regardless of differing inundation lengths.

Two of the investigated tree species were common to both forests: *Pterocarpus amazonum* resided in the highest-elevated plots (MA and TA) and *Macrolobium acaciaefolium* was present in the lowest-elevated plots (TN and MH). Both species developed the same basic type of root pattern in both forests (Figs. 8.5 and 8.6). However, they differed considerably in their relative total length, which was lower in the igapó than in the várzea (*P. amazonum* 31.4 and 59.2, *M. acaciaefolium* 44.6 and 52.2, respectively). Both species developed a higher number of short roots in the Igapó, the value for *M. acaciaefolium* being the highest one for all investigated root systems (*P. amazonum* 9.6 and 5.5, *M. acaciaefolium* 18.8 and 5.1, respectively).

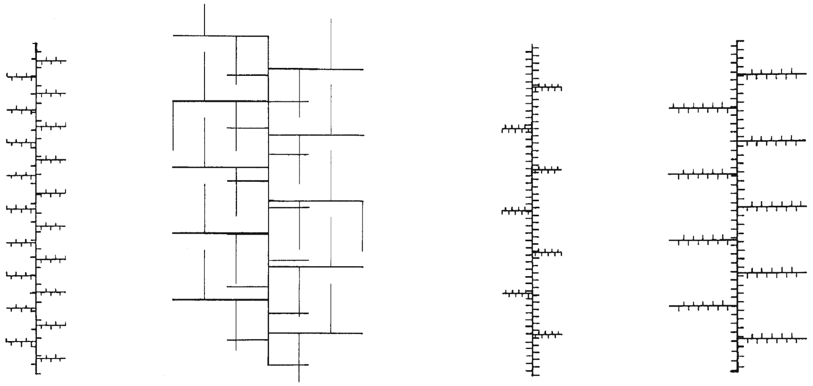


Cynometra spruceana
(Caesalpinaceae)
(TA, TH, TN)

Amphirrox surinamensis
(Violaceae)
(TA, TH)

Macrolobium acaciaefolium
(Caesalpiniaceae)
(TN)

Elvasia callophylla
(Ochnaceae)
(TH, TN)



Matayba macrolepis
(Sapindaceae)
(TA, TH)

Duroia species
(Rubiaceae)
(TH, TN)

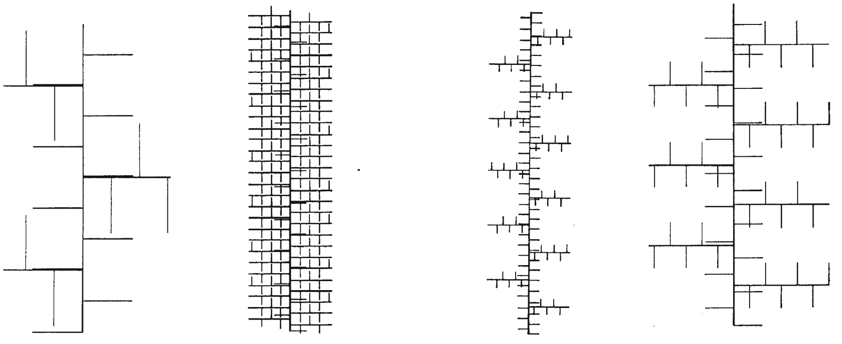
Pterocarpus amazonum
(Fabaceae)
(TA)

Mora paraensis
(Casalpinaceae)
(TA)

Fig. 8.5 Schematic depictions of root branching patterns in the igapó

8.4.5 Mycorrhizal Associations

In the igapó forest, 89% of the 44 investigated tree species were infected by AM-fungi, 2% were associated with EM, and 9% were symbiotically inactive. The ectomycorrhizal infection was diagnosed on the commonly occurring tree species *Aldina latifolia* (Fabaceae) (31% in TA, 6% in TH). These roots were almost inseparably attached to litter fragments (Fig. 8.7), a phenomenon not identified for AM roots. The non-mycorrhizal roots, detected only in the medium (TH) and lowest elevated (TN) plots, were characterised by little branching and relatively large root diameters (0.8–1.3 mm). The 26 tree species tested in the várzea forest predominantly associated with the AM-type (88%). The remainder of the várzea species were symbiotically inactive. One non-mycorrhizal tree species was present in each of the várzea plots; in the long inundated plot (MH) it

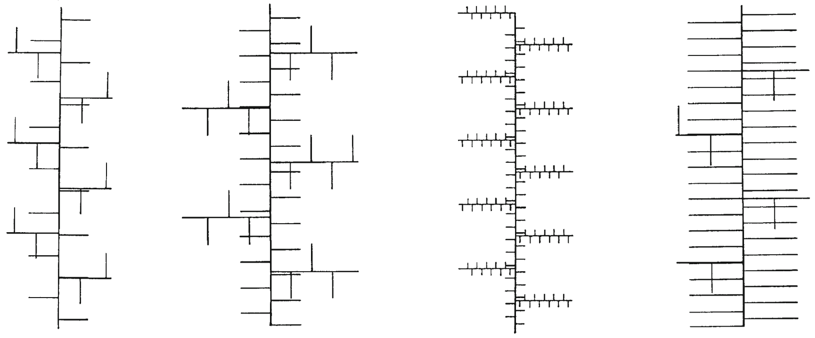


Labatia glomerata (Sapotaceae) (MA, MB, MH)

Triplaris surinamensis (Polygonaceae) (MA, MB)

Macrolobium acaciaefolium (Caesalpiniaceae) (MA, MH)

Gustavia augusta (Lecythidaceae) (MA)



Simaba guianensis (Simaroubaceae) (MH)

Alchornea schomburgkii (Eurphorbiaceae) (MH)

Pterocarpus amazonum (Fabaceae) (MA)

Pseudobombax munguba (Bombacaceae) (MA, MB,MH)

Fig. 8.6 Schematic depictions of root branching patterns in the várzea

was the frequently occurring species *Crataeva benthamii*. None of the examined várzea roots were infected by EM.

8.5 Discussion and Conclusions

The fine root systems of the várzea and igapó forests differed profoundly in their amount, depth distribution, production rates and root branching patterns. This points to different foraging strategies employed by tree roots to cope with conditions of low soil fertility. Mechanisms involved include an increase in root density within localised nutrient-rich soil patches (Blair and Perfecto 2001). The formation of superficial root mats has, for example, often been observed within organic-rich soil layers of tropical forests (Laclau et al. 2004). The proportion of fine roots may

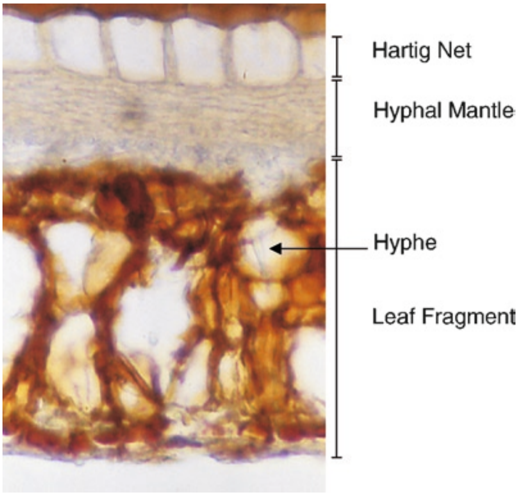


Fig. 8.7 Ectomycorrhizal symbiosis with *Aldina latifolia* (igapó)

further be enhanced, since fine roots are generally better suited to absorb nutrients than their thicker counterparts (Blair and Perfecto 2001).

While a lower above-ground tree biomass was observed in the igapó relative to the várzea forest, higher fine root concentrations were detected in the igapó topsoils (Fig. 8.2). This is in accordance with previous studies conducted on nutrient-poor tropical as well as temperate-zone forests (Meyer 1967; Scherfose 1990; Priess et al. 1999), since infertile soil conditions generally impose a selective pressure for maximization of the absorptive root surface area (Paz 2003).

Ecosystem stability under infertile soil conditions may be achieved through short circuited nutrient cycles (Vitousek 1982; Anderson and Swift 1983; Sayer et al. 2006). This nutrient cycling is often closely linked to the soil organic matter pool, which upon decomposition contributes greatly to the plant-available nutrient contents (Vitousek 1982). Leaching losses of nutrients may subsequently be diminished by means of an efficient root capturing system. Rapid ion uptake may further circumvent nutrient losses via leaching or fixation into plant-unavailable chemical forms. Such nutrient conserving mechanism is crucial for ecosystem stability in the igapó region, while short circuited nutrient cycling is not a matter of survival for the nutrient-rich várzea forest.

The vertical distribution of fine roots generally followed trends in soil fertility. Although highest nutrient concentrations corresponded to the litter layers of both forests, their availability was less relative to the underlying organic-rich soil horizons. This was due to lower mineralization rates, as indicated by higher C/N ratios, in the litter layers (Table 8.1). The preferred rooting depth was therefore associated with the organic-rich Ahh-horizons of both forests. Limited nutrient availability subsequently restricted the proliferation of fine roots into the lower soil mineral layers of the igapó forest (Fig. 8.3). In contrast, the fine root system of the nutrient-rich várzea forest extended to 43 cm soil depth (Fig. 8.3). The second peak in fine root concentration at 38–43 cm soil depth in the várzea forest did not coincide with an increased nutrient supply (Table 8.1), but was rather caused by a change in soil texture from loamy clay to silty sand (data not shown), the latter being more easily penetrated by roots.

Despite lower root production rates (Fig. 8.4), the fine root length densities of both dead and living roots were higher in the igapó than in the várzea forest (Fig. 8.2). The elevated concentration of living roots pointed to a higher root longevity in the igapó forest, which was interpreted as an adaptation to low nutrient supply by means of an efficient use of energy. Similarly, long life spans of root systems have often been documented in nutrient-poor temporal forest ecosystems (Chapin and van Cleve 1981; Nadelhoffer et al. 1985; Trappe and Fogel 1977). The higher concentrations of dead roots in the igapó as compared to the várzea forest were caused by slower litter decomposition. It is noteworthy that the decomposition coefficients in the igapó were approximately half of those in the várzea (Meyer 1991). In contrast, the lower root concentrations, in spite of higher production rates, resulted from faster root turnover rates in the várzea relative to the igapó forest.

An increase in root length density with increasing inundation length was prominent in the igapó forest (Fig. 8.2). Prolonged flooding apparently favoured the formation of higher root concentrations to compensate for short optimal growth conditions. The zoning of vegetation along the catena suggested the selective establishment of certain tree species (Table 8.2), with differing root production abilities, according to inundation length.

The detection of a constant amount of living roots between the start and end of the emerse phase (Fig. 8.2) was interpreted as tolerance mechanism to flooding conditions. Such tolerance is generally of physiological nature and stems from the change of aerobic to anaerobic metabolism under waterlogged soil conditions (Schlüter 1989; Haase and Rätsch 2010).

The root systems in the igapó forest exhibited a higher geometric diversity than those of the várzea forest. Extremely high numbers of short roots were frequently detected in the igapó forest (Fig. 8.5), while the relative total lengths of várzea tree roots were significantly higher (Fig. 8.6). Since intensive branching allows for a more thorough exploitation of the soil nutrient reserves, igapó tree roots were better equipped to retain nutrients within the ecosystem. In addition, thinly-spaced branching enables roots to better influence the nearest rhizosphere chemically than can widely-spaced root systems, since root exudates are more diluted in the rhizosphere of the latter branching type (Gardner et al. 1983a,b; Fischer et al. 1989).

It should further be noted that the physiological root diversity was greater in the igapó forest. The totality of the different root branching types in the igapó forest thus, allowed for a more complete foraging of the soil nutrient pool. For instance, soil micro-sites unoccupied by highly branched root systems may be sought out by tree roots displaying other root branching types, such as the *Duroia* type (Fig. 8.5).

The fine root branching types identified for both forests were most probably genetically determined, since the general branching types remained similar for tree species common to both forests. Slight modifications of the branching types, however, resulted from differences in the soil nutrient regimes.

Most tree species associated with AM in both forests. The majority of AM symbioses with tropical trees has been documented in many studies (Redhead 1980; Janos 1983; da Silvia et al. 2001), however, some tropical trees may be infected by EM (Malloch et al. 1980; Janos 1983; Alexander and Höberg 1986; Högberg and Piearce 1986; Alexander 1989). In tropical forests located on infertile soils, EM may be more abundant than AM by virtue of their better nutrient scavenging abilities (Janos 1983). The proposal by Singer and Araujo (1986) that EM associate with the dominant tree species of the igapó forest was, however, not confirmed by this study. Only one tree species, *Aldina latifola*, was diagnosed to form ectomycorrhizal associations and was with a total of 11 individuals on the TA and TH plots not the principal tree species. While Singer and Araujo (1986) also detected EM on *Aldina latifolia*, they further documented ectomycorrhizal associations with *Swartzia polyphylla*. The latter tree species was in this study AM diagnosed. Likewise, Moyersoen et al. (2001) tested the hypothesis that EM may be more abundant than AM in tropical heath forests. In their study conducted on a Venezuelan caatinga, the most dominant tree species associated, however, with AM.

The co-occurrence of EM and AM tree species may be attributed to the occupation of different soil niches (Moyersoen et al. 2001). For instance, EM may have a selective advantage of accessing phosphorus from organic sources (Alexander 1989; Moyersoen et al. 2001), such as by secretion of chelators which increase P solubility (Cromack et al. 1979; Szaniszlo et al. 1981). The finding that EM were almost inseparably attached to litter fragments (Fig. 8.7) suggests the extraction of organically derived phosphorus.

Investigation of fine root length densities, branching systems and the production rates of fine roots in the nutrient-poor igapó as compared to the nutrient-rich várzea forest, lead to the following conclusions. The igapó has three strategies to meet the low nutrient reserves of its site:

- Firstly, it develops higher concentrations of fine roots in the soil relative to the várzea forest. This results in shorter pathways for nutrient uptake by roots.
- Secondly, the higher root longevity of igapó roots allows for an economic use of assimilates.
- Thirdly, the more diversified branching systems of fine roots result in a more thorough exploration of the soil nutrient reserves.

The proposal by Singer and Araujo (1986) that the igapó forest should be viewed as an ectotrophic forest could not be confirmed by this study, as most of the tree species were symbiotically associated with the AM-type in both forests.

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Chapter 9
Morphology and Anatomy of Leaves

Danielle Waldhoff and Pia Parolin

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Abstract Leaves are among the most important organs of a plant, and they are indicators of the condition of a tree. Their morphology and anatomy shows adaptations and their functional traits reflect to some extent the constraints of the environments where the plants typically grow. However, despite the big differences in flooding intensity and nutrient availability, leaves of Amazonian floodplain trees are similar in their morphoanatomy and exhibit traits which are generally considered as xeromorph, just as the leaves of upland species. The xeromorphic leaf structure may represent a pre-adaptation resulting from the dry habitats most tree species originate from. It also helps to cope with insufficient water supply to the tree crowns

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during the aquatic phase which is caused by a decrease of root functioning due to waterlogging and submergence. The assimilation organs perform perfectly well despite the long periods of waterlogging or complete submergence in darkness. Leaf structure does not reflect the extreme environmental conditions to which trees in Amazonian floodplains are subjected. No patterns could be detected of a relationship of leaf functional traits with flooding intensity and nutrient availability.

9.1 Introduction

Long lasting inundations affect the physicochemical conditions in the soil, with oxygen deficiency in the rhizosphere and resulting stresses (Haase and Rätsch 2010) 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.

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

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

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

Thus, the aim of this chapter is to describe the leaf characteristics of Amazonian floodplain trees, to analyse the reactions to flooding of parameters related to the assimilation organs and to discuss the variation in response to flooding. In the whole chapter we deal with leaves which were not newly developed under water but which were already present at the start of the flooding event.

9.2 Leaf Lifespan and Age

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

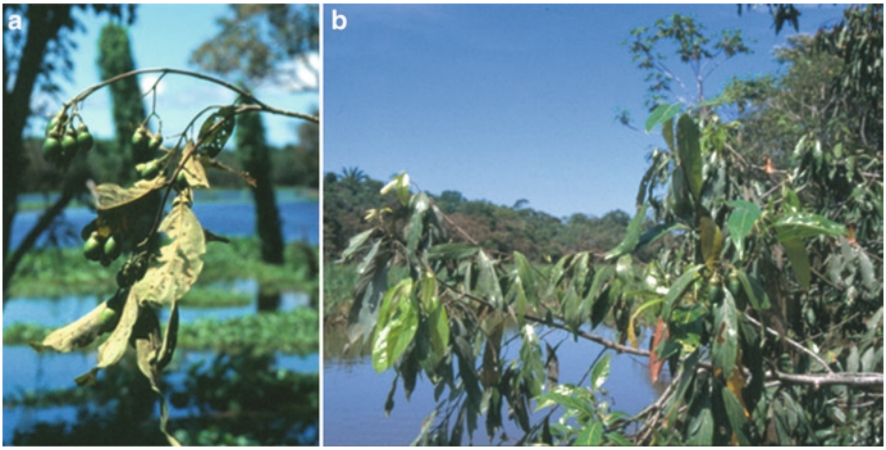

Fig. 9.2 Branch of *Nectandra amazonum*: Leaf shedding and replacement occurs continuously, but a period with clearly senescent leaves (**a**) and fruit maturation dominates in the beginning of the aquatic period, whereas new leaves are flushed (**b**) at the highest water peak and towards the end of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

9.3 Xeromorphism

The leaves of Amazonian floodplain trees exhibit traits which are generally considered as xeromorph (Medina 1983; Roth 1984; Bolhàr-Nordenkampf and Draxler 1993; Waldhoff et al. 2002; Waldhoff 2003): large epidermal cells (*Hevea spruceana, Eugenia inundata,* Fig. 9.3a), thick outer epidermis walls (*Rheedia brasiliensis* Fig. 9.3b, *Himatanthus sucuuba*), thick cuticle (*Eschweilera tenuifolia, Simaba guianensis*), compact spongy parenchyma with only few and small intercellular spaces (*Senna reticulata* Fig. 9.3c, *Licania apetala*), sunken stomata (*Vitex cymosa, Pouteria glomerata*), and transcurrent vascular bundles with a strong sclerenchymatous bundle sheath (*Nectandra amazonum, Eugenia inundata*).

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

Xeromorphism can also be a response to drought (Medina 1983; Medina et al. 1990). Xeromorphic characters of all leaf types indicate that the trees experience drought stress in their floodplain habitats, independent of leaf-fall behaviour. This at a first glance is astonishing, because the trees grow during several months in flooded or waterlogged soils and during the remaining time drought stress seems to be moderate because of a high groundwater table in the floodplain and/or sporadic rainfall. However, the significance of xeromorphism as an adaptation to drought and/or nutrient deficiency

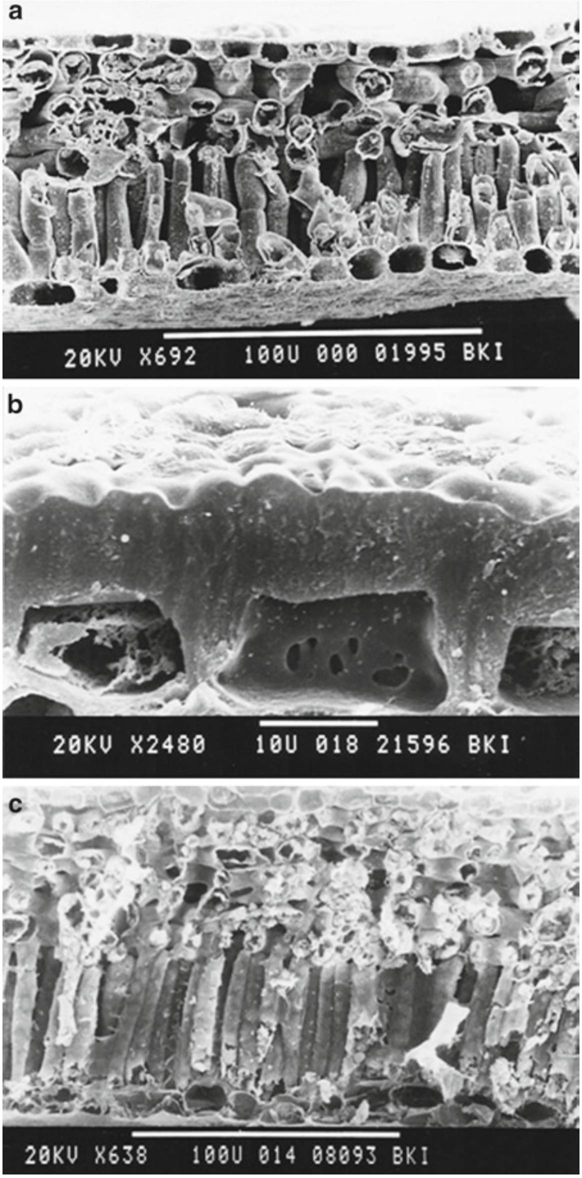

Fig. 9.3 Leaf anatomy: (**a**) *Eugenia inundata* cross section with large epidermal cells; (**b**) *Rheedia brasiliensis* thick outer epidermis walls; (**c**) *Senna reticulata* compact spongy parenchyma with only few and small intercellular spaces

in central Amazonian floodplains remains elusive. Xeromorphic leaves are reported to be a general feature in tropical forests (Roth 1984). Worbes (1986, 1997) reported on water deficit in the canopy of central Amazonian floodplain forests during the inundation period similar to the one found in trees on terra firme during the dry season.

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

9.4 Anatomy of Leaves

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

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

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

9.5 Stomata

Stomatal density at the lower leaf side of 34 analysed tree species varied between 25 and 2,339 mm^{-2} (Table 9.3) and did not differ significantly between species that keep or shed submerged leaves (Waldhoff 2003). Species with higher stomatal

Table 9.1 Cell size in different leaf components (all measures in μm). Epidermis cells, width × 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		
Aldina latifolia	Large	Large	Medium	Thick	Medium	Medium
Alchornea sp.	Small	Small	Medium	Medium	Long/small	Medium
Alibertia sp.	Large	Small	Thick	Thin	Medium/small	Medium
Bactris bidentula	Small	Small	Thick	Thick	Medium	Small
Bactris maraja	Medium+	Medium	Thick	Medium	Not existing	Medium
Calliandra amazonica	Medium	Medium	Thick	Thick	Very long/small	Small
Crateva benthami	Large	Small	Medium	Thick	Small	Small
Cecropia latiloba	Large	*	Thin	*	*	*
Cassia leiandra	Medium	Medium	Thin	Thin	Small	Small
Couepia paraensis	Large	Medium	Thick	Medium	Medium/small	Not existing
Eugenia inundata	Large	Small	Thick	Thin	Medium	Medium
Eschweilera tenuifolia	Medium	Small	Very thick	Thick	Long/small/small	Medium
Hevea spruceana	Very large	Large	Thick	Thin	Very long	Medium
Himatanthus sucuuba	Large		Thick	Thin		
Ilex inundata	Medium	Small	Thick	Thick	Very long/small	Small
Licania apetala	Large	(Papilla)	Medium	(Papilla)	Long/small/small	Medium
Macrolobium acaciifolium	Large	Medium	Thick	Thin	*	Medium
Maprounea guianensis	Medium	Large	Thick	Thin	Long	Small
Mouriri guianensis	Small	Small	Thick	Thin	Small	Large
Nectandra amazonum	Large	Large	Medium	Medium	Long/small/small	Not existing
Nectandra sp.	Large	Large	Thick	Thick	Medium/small	Large

(continued)

Table 9.1 (continued)

Species	Epidermis cell size		Outer wall – cuticula		Palisade parenchyma cell size	Spongy parenchyma cell size
	ue	le	ue	le		
Ouratea hexasperma	Large	Medium	Very thick	Medium	Very long	Medium
Psidium acutangulum	Large +	Small	Thick	Thin	Medium/small	Medium
Pouteria glomerata	Small	Small	Thick		Medium	Small
Pseudobombax munguba	Large	Medium	Thin	Medium	Long/small	Small
Quiinia rhytidopus	Medium	Small	Thick	Thin	Medium	Medium
Rheedia brasiliensis	Large	Large	Very thick	Thick	Medium/small	Medium
Simaba guianensis	Large	Small	Thin	Thick	Medium	Small
Salix humboldtiana	Medium+	Medium	Thin	Thin	Small/small etc.	Not existing
Senna reticulata	Medium	Medium	Thin	Thin	Long	Medium
Tabebuia barbata	Medium+	Large	Thin	Thin	Long-very long	Medium
Tabernaemontana juruana	Large	Large	Thick	Thick	Small	Large
Tovomita macrophylla	Large	Large	Thick	Thick	Small	Small
Vitex cymosa	Large	Large	Thin	Thin	Long/small/small	Not existing

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

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
Aldina latifolia	1	Very compact		Some transcurrent	Weekly developed
Alchornea sp.	1 up, 1 low	Very compact		Some transcurrent	Weekly developed
Alibertia sp.	2	Compact		Not transcurrent	Weekly developed
Bactris bidentula	1	Compact		Not transcurrent	Sheath surrounding the bundle, fibres
Bactris maraja	Not existing	Compact		Not transcurrent	Sheath surrounding the bundle, fibres
Calliandra amazonica	1 up, 1 low	Loose		Not transcurrent	Weekly developed
Crateva benthami	1–2	Loose		Not transcurrent	No sclerenhyma
Cecropia latiloba	*	*		*	*
Cassia leiandra	1	Compact		Transcurrent	Strong sheath surrounding the bundle
Couepia paraensis	4	–		Transcurrent	Capping bundles on both sites
Eugenia inundata	1	Regular		Transcurrent	Capping bundles on both sites
Eschweilera tenuifolia	1 up, 1 low	Very compact		Mostly transcurrent	Sheath surrounding the bundle
Hevea spruceana	1	Compact	Laticifirous	Not transcurrent	Weekly developed
Himatanthus sucuuba	*	*		*	*
Ilex inundata	2	Regular		Not transcurrent	Capping bundles on one site
Licania apetala	2	Very compact		Not transcurrent	Strong sheath surrounding the bundle
Macrolobium acaciifolium	*	Regular		*	*
Maprounea guianensis	1	Regular		Transcurrent	Strong sheath surrounding the bundle
Mouriri guianensis	1	Regular		Not transcurrent	Strong sheath surrounding the bundle

(continued)

Table 9.2 (continued)

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

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)

	Density (number mm^{-2})		
Species	ue	le	Form
Aldina latifolia		25	Sunken in thick cuticula
Alchornea sp.	309	233	Not sunken
Alibertia sp.		696	Not sunken
Bactris bidentula		nv	Completely sunken in cuticular folds
Bactris maraja	63	248	Sunken
Calliandra amazonica		643	Sunken in thick cuticula
Crateva benthami		582	Not sunken
Cecropia latiloba	69	?	Not sunken
Cassia leiandra		814	Sunken
Couepia paraensis		nv	Sunken in cuticular folds, hidden by hairs
Eugenia inundata		620	Sunken in cavity formed by the raised stomatal rim
Eschweilera tenuifolia		nv	Sunken in very thick cuticula
Hevea spruceana		369	Sunken
Himatanthus sucuuba		675	Sunken, with raised stomatal rim
Ilex inundata		601	Sunken with raised stomatal rim
Licania apetala		nv	Sunken in deep pit formed by papillose subsidiary cells
Macrolobium acaciifolium	nv	nv	le: sunken between elevations of wax
Maprounea guianensis		nv	Sunken in cuticular folds
Mouriri guianensis		1,952	Sunken in holes formed by cuticular folds
Nectandra amazonum		1,188	Sunken
Nectandra sp.		318	Sunken in cuticula
Ouratea hexasperma		913	Sunken in cavity formed by the raised stomatal rim
Psidium acutangulum	149	837	Sunken in cavity formed by the raised stomatal rim
Pouteria glomerata	177	449	ue: not sunken, le: sunken with raised stomatal rim and long, narrow aperture
Pseudobombax munguba	nv	284	Sunken with raised stomatal rim
Quiinia rhytidopus		2,339	Sunken in deep pit formed by papillose subsidiary cells
Rheedia brasiliensis	nv	178	Sunken in pit formed by very thick cuticula
Simaba guianensis		4	Sunken
Salix humboldtiana	393	343	Sunken with raised stomatal rim
Senna reticulata	141	84	Sunken
Tabebuia barbata		287	Sunken with raised stomatal rim
Tabernaemontana juruana		716	Not sunken
Tovomita macrophylla		201	Not sunken
Vitex cymosa		176	Sunken in cavity formed by the raised stomatal rim

le, lower epidermis; nv, not visible; ue, upper epidermis densities tended to show small epidermal cells (e.g. *Mouriri guianensis, Ouratea hexasperma, Quiinia rhytidopus*) and vice versa (e.g. *Acmanthera latifolia, Tabernaemontana juruana, Tovomita macrophylla*). Stomatal densities were apparently not associated with a certain type of leaf-fall behaviour, which corresponds with the literature on the relation of stomatal density with xeromorphism (Wilkinson 1979; Roth 1984; Bolhàr-Nordenkampf and Draxler 1993; Cao 2000; Dong and Zhang 2000). While hypostomatic leaves represent the usual pattern among dicotyledonous trees, additional stomata at the upper leaf side may have emerged as an adaptation to dry habitats in some species (Bolhàr-Nordenkampf and Draxler 1993), e.g. *Rheedia brasiliensis* (Fig. 9.4a), *Bactris maraja*, *Pouteria glomerata*, and *Psidium acutangulum* (Fig. 9.5). Amphistomatic leaves are commonly found in members of the family Caesalpiniaceae (Roth 1984; Metcalfe and Chalk 1950).

Most of the analysed species had sunken stomata at the lower side of the leaf (Fig. 9.4b; Waldhoff 2003), some even had stomata that are not visible because they

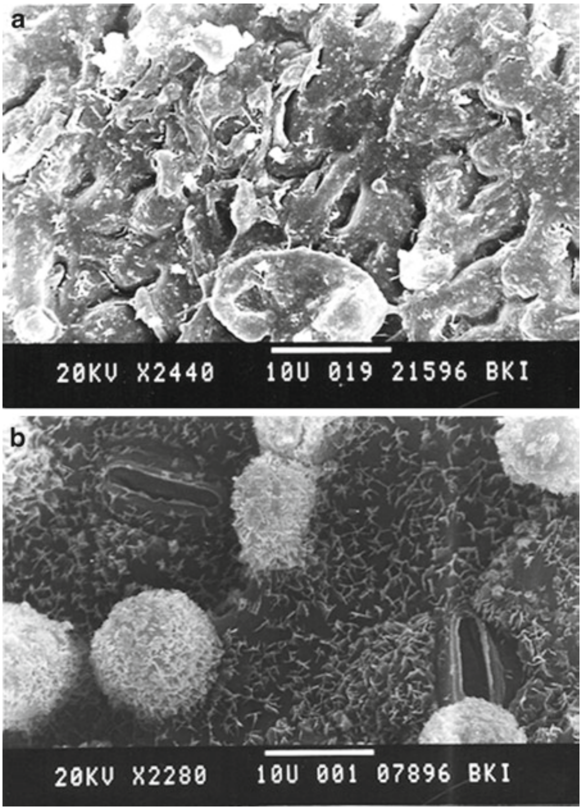

Fig. 9.4 *Rheedia brasiliensis* stomata on the upper leaf side (**a**); sunken stomata on the lower side of the leaf in *Cassia leiandra*, with wax crystals (**b**)

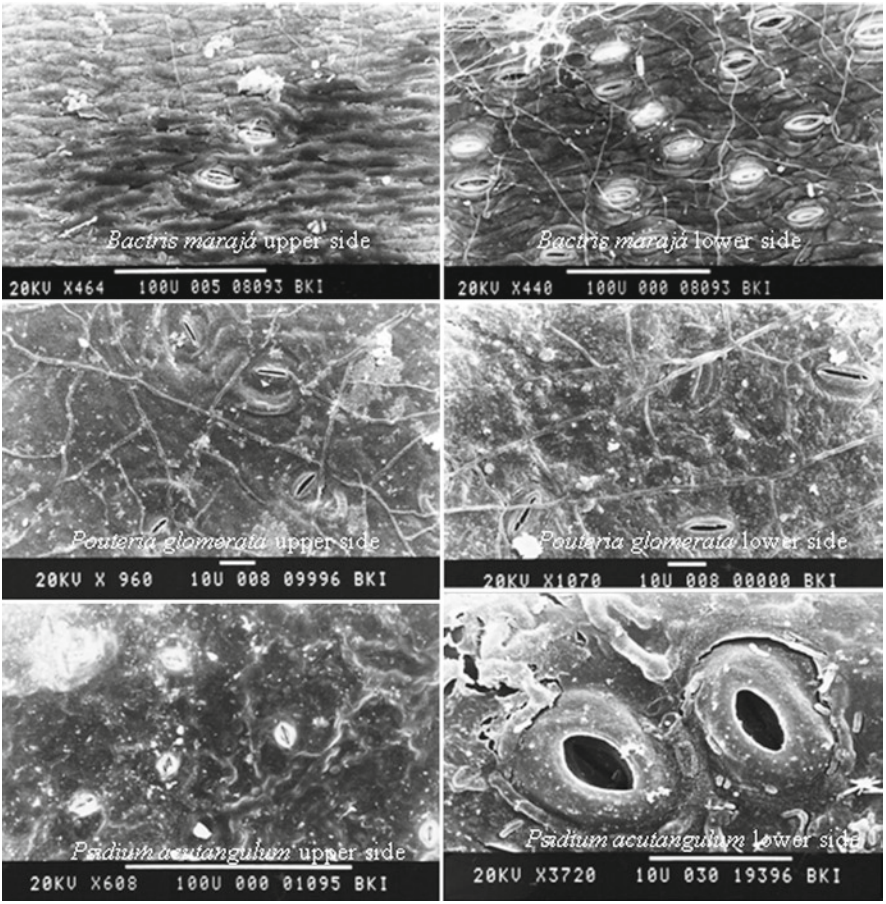

Fig. 9.5 Upper (*left*) and lower (*right*) leaf side of *Bactris maraja*, *Pouteria glomerata*, and *Psidium acutangulum*

are buried in a cavity or pit-like hole, sunken between waxy elevation or cuticular folds (Table 9.3).

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

Sunken stomata are common in xeromorphic leaves (Roth 1984; Bolhàr-Nordenkampf and Draxler 1993). On the other hand Fahn and Cutler (1992) reported that only 34% of xeromorphic species (35 dicotyledons, 33 monocotyledons, 3 gymnosperms) from arid and semi-arid environments possess sunken stomata. Lindorf (1993) studied 17 tree species from Venezuelan tropical rainforests and found no species with sunken stomata. From this perspective the presence of sunken stomata in 27 out of 34 species studied seems remarkable.

9.6 Surface Structures

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

Ten analysed species exhibited wax deposits (Fig. 9.7), twenty showed cuticular ornamentations, mostly on the lower leaf side (see Table 9.4). These ornamenta-

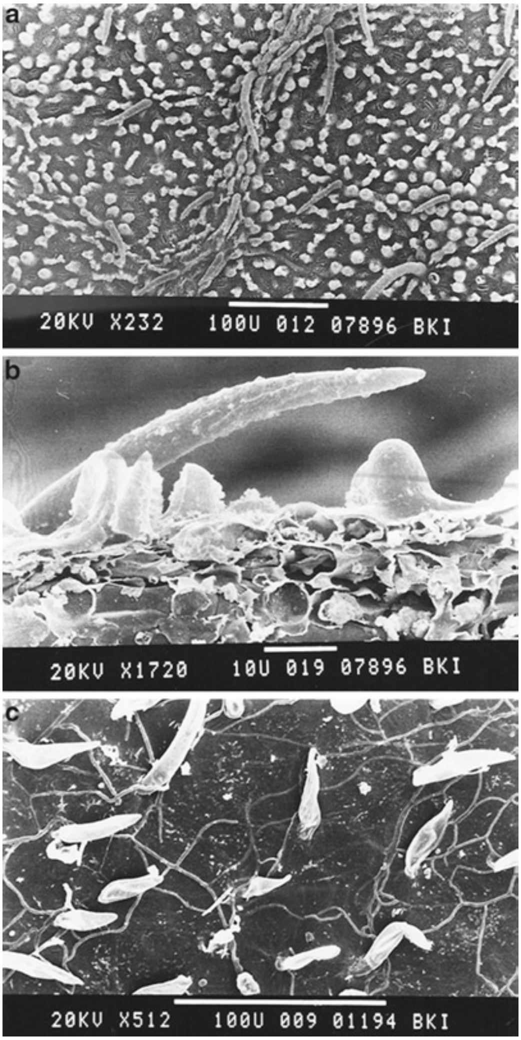

Fig. 9.6 Leaf surface structures: hairs and papillae (**a**, cross section **b**) on lower leaf surface of *Cassia leiandra*, hairs on upper (**c**) and lower (**d**) leaf side of *Nectandra amazonum*, and lower leaf side (**e**) of *Pouteria glomerata*

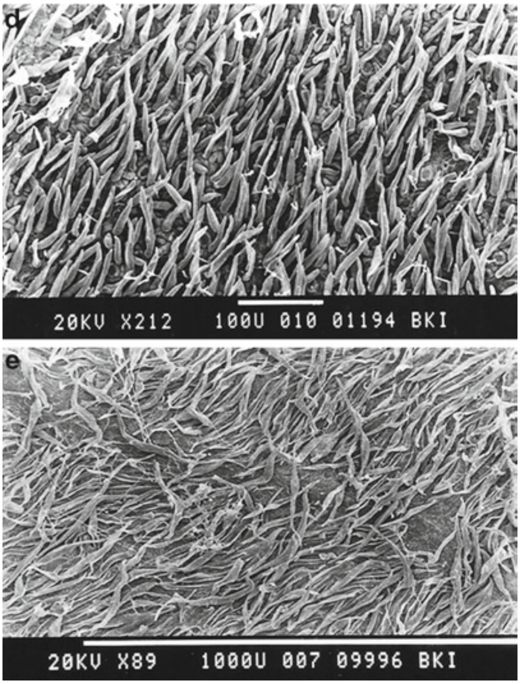

Fig. 9.6 (continued)

tions 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). 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).

9.7 Chloroplasts

In the palm *Bactris bidentula*, palisade parenchyma cells are densely filled with chloroplasts (Waldhoff 2003). Such a high density of chloroplasts in palisade parenchyma had not been described hitherto. It might be helpful for a possible photosynthesis under water when light is the limiting factor (Furch et al. 1985). Although light can be an important limiting factor under water, presumably CO_2 is

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

	Hairs				
Species	Not glandular	Glandular	Papillae	Wax layer	Cuticular ornamentation
Aldina latifolia	le				le: rough surface with irregular elevations
Alchornea sp.					ue: radiating striae around stomata
Alibertia sp.					le: rough surface
Bactris bidentula				le	ue, le: the whole surface is structured by many cuticular folds
Bactris maraja	le				ue, le: the whole surface is structured by some cuticular folds
Calliandra amazonica	ue				
Crateva benthami					ue, le: the whole surface is structured by many cuticular folds
Cecropia latiloba	ue; le: filamentous hairs	ue			
Cassia leiandra	le		le: simple, corn-like	ue, le: upright scales	
Couepia paraensis	le				le: cuticular folds; ue: very large cuticular folds
Eugenia inundata		ue, le: glandular scales			le: concentric rings of striae around stomata and radiating striae around concentric rings ue: striae random and very dense
Eschweilera tenuifolia		ue, le: glandular scales			

Hevea spruceana				le	ue, le: reticulum of crests and buttressed ridges around stomata
Himatanthus sucuuba					le: concentric rings of striae around stomata
Ilex inundata				ue	le: concentric rings of striae around the stoma
Licania apetala			le: with dense pappilose hairs		
Macrolobium acaciifolium		ue		ue: many elevations	
Maprounea guianensis				ue: many elevations	le: dense network of radiating striae around the stoma and between them
Mouriri guianensis					le: dense network of cuticular folds
Nectandra amazonum	ue, le			le: rods of wax	
Nectandra sp.					
Ouratea hexasperma				ue, le	le: elevations formed by cuticula
Psidium acutangulum	le				ue, le: cuticula forms puzzle like structures
Pouteria glomerata	le				le: dense and complex network of undulate striae
Pseudobombax munguba		le: nectaries			le: concentric rings of striae around the stoma, and radiating striae around concentric rings

(continued)

Table 9.4 (continued)

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

ue, upper epidermis; le, lower epidermis

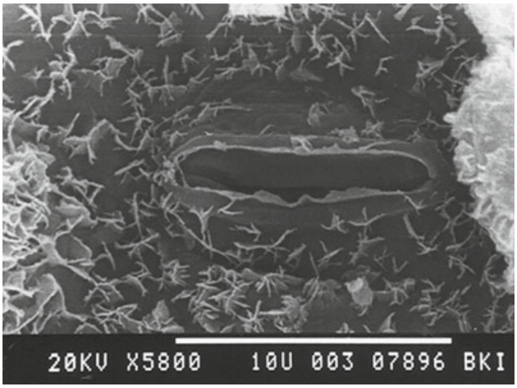

Fig. 9.7 Leaf surface structures: wax crystals and stoma on lower leaf surface of *Cassia leiandra*

much more limiting (Mommer and Visser 2005), but no studies are available to this respect in Amazonian floodplain trees.

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

9.8 Specific Leaf Mass

Specific leaf mass was higher in waterlogged months in many species, e.g. *Cecropia latiloba*, *Nectandra amazonum*, *Senna reticulata*, *Tabebuia barbata*, and *Vitex cymosa*, in adult trees in the field as well as in seedlings under experimental conditions (Parolin 2002d). Specific leaf mass in the non-flooded period varied between 48.8 $\mathrm{gm^{-2}}$ for the pioneer *Senna reticulata* and 118.9 $\mathrm{gm^{-2}}$ for the evergreen non-pioneer *Nectandra amazonum* (Table 9.5). In waterlogged months, specific leaf mass in an average was 5–33% higher than in non-flooded months. Only *Crateva benthami* had significantly lower specific leaf mass with waterlogging. This was due to the fact that the new leaves – which were mainly produced in the aquatic period – had higher specific leaf mass than older leaves. In *Cecropia latiloba*, *Crateva benthami*, *Tabebuia barbata* and *Vitex cymosa* there was a constant increase of specific leaf mass in the first months after leaf expansion, which occurs in the last months of the flooded period.

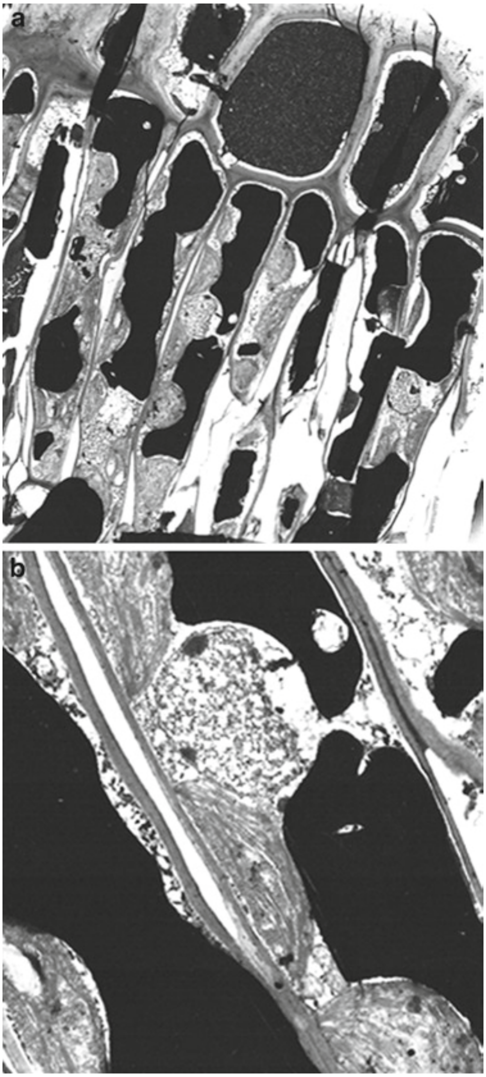

Fig. 9.8 Cross-sections from a leaf of *Symmeria paniculata* submerged at 1m depth: (**a**) Epidermis cells (upper row) and palysade parenchyma (lower row; starch grain); (**b**) chloroplast (upper organelle) and nucleus (middle organelle) from palisade parenchyma cell (transmission electron microscopy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

9.9 Leaf Size

The size of single leaves varied between few cm^2 for *Salix* and more than 2,380 cm^2 for *Cecropia latiloba* (Table 9.5). The pioneer *Senna reticulata* and two deciduous non-pioneers (*Crateva benthami*, *Tabebuia barbata*) had highly significant

Table 9.5 Specific leaf mass and leaf area 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

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

reductions of leaf area (25–37%) in the aquatic period, compared to the terrestrial period (Table 9.5). *Cecropia latiloba* and *Nectandra amazonum* produced leaves with a more or less constant size throughout the year.

Reductions of leaf size were caused by leaf senescence and a subsequent loss of leaflets. Only in *Senna reticulata* leaf size reduction was a direct response to water stress: in waterlogged months, the newly produced leaves and leaflets were smaller than in the terrestrial period (Parolin 2001c) (Fig. 9.9). Data in this study indicate a periodicity in several leaf traits which changes parallel to the flooding periodicity, but which is determined primarily by leaf age and senescence and only indirectly by flooding. The timing of the changes of specific leaf mass and leaf size was similar between species and was concentrated in the aquatic period, but the degree of changes differed among the species. Leaves of pioneer and non-pioneer species, and leaves of deciduous and evergreen species did not show a uniform trend, characteristic for certain growth strategies, as response to flooding. Apparently differences were closely linked to leaf age and cannot be considered as adaptive to the changing hydrological conditions.

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

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
C. latiloba	55.2–83.3	73.6 ± 5	71.8 ± 5	−2.6	n.s.
S. reticulata	57.0–84.4	71.0 ± 5	64.5 ± 4	−9.2	***
N. amazonum	30.9–59.0	48.6 ± 4	48.5 ± 4	−0.2	n.s.
C. benthami	49.4–81.4	67.6 ± 5	61.5 ± 6	−9.1	***
T. barbata	30.3–80.8	62.7 ± 5	54.7 ± 11	−12.8	***
V. cymosa	44.8–90.8	62.7 ± 9	55.0 ± 7	−12.3	***

*$p \geq 0.05$; **$p \geq 0.01$; ***$p \geq 0.001$; n.s. not significant

9.10 Leaf Water Content

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

9.11 Discussion and Conclusions

Most measured parameters and their changes in the annual cycle do not reflect the extreme environmental conditions to which trees in Amazonian floodplains are subjected. The hydrological conditions in the floodplains are unfavourable for tree growth for several months every year, as indicated by regular growth reductions in the wood (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. Leaf anatomy is not particularly divergent between species. Common to most species are a xeromorphic character, large upper epidermis cells, long palisade parenchyma cells, small spongy parenchyma cells, sunken stomata, hairs and wax layers on the leaf surface.

Amazonian floodplains show all characteristics of extreme sites. A very long uninterruted period of flooding with a high amplitude, rapid changes of water level, anoxic conditions in the rhizosphere, high sedimentation in várzea, lack of nutrients in sediment-poor igapó, high mechanical stress and even drought lead to difficult conditions for growth of all organisms living in this ecosystem. Nevertheless, the high diversity of species and life strategies may result from the fact that this extreme site has only a reduced number of factors representing stress for the trees, and the regular disturbances may even represent a driving force for resistance and adaptive evolution. The high complexity of the system and the short but regular occurrence of factors enhancing tree growth allow the formation of highly diverse survival strategies. The species are seldom highly specialized – most have high ecological amplitudes. In these floodplains, specialization is low enough to allow the trees to react to changing environmental conditions, and is high enough to allow a high diversity along the hydric and edaphic gradient.

Chapter 10
Gas Exchange and Photosynthesis

Pia Parolin, Danielle Waldhoff, and Maria T.F. Piedade

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Abstract Gas exchange and photosynthetic activity give insight into the energy balance of plants. These parameters, as well as transpiration, stomatal conductance, intercellular CO_2 concentrations, leaf chlorophyll and nitrogen contents, are especially interesting because they can be measured directly on the living organs

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and thus make statements possible about the physiological condition of a trees in different hydric conditions. Photosynthetic assimilations measured under natural conditions in Amazonian floodplains lie in the same range as those of other tropical woody plants. Responses to waterlogging show decreases: overall means of physiological parameters are higher in the non-flooded period in most analysed species, but many trees also perform the highest absolute values of CO_2 assimilation in the aquatic phase. Like in other wetland species, flooding in many Amazonian floodplain species enhances stomatal conductance, leaf water potential and net photosynthesis, especially under conditions leading to high air-vapour pressure deficits. The tree species developed a high diversity of adaptive strategies, with tight regulation of water and carbon relations under severe soil-oxygen deficiencies. This may allow them to cope with flooding and even drought problems and permit high photosynthetic activities during most of the year, and thus gives these species the dominance over natural competitors which may be more efficient under non-flooded conditions but are unable to compete when inundated.

10.1 Introduction

Long continuous inundations affect the physicochemical conditions in the soil and thus the roots of the trees. Continuous investigations of the rhizosphere are extremely difficult and hardly feasible during the entire annual cycle in adult trees due to the high periodic water level fluctuations. Therefore, other parameters are used as indicators for the reactions of the trees to flooding. Clear indicators of the condition of a tree are its assimilation organs (Medina 1984). Parameters such as photosynthetic activity, chlorophyll and nitrogen contents can be measured directly on the living organs. Since photosynthesis and the leaves' physiological condition are crucial for the energy balance of the trees, these parameters make statements possible about the physiological condition of the trees.

Out of the large variety of tree species growing in Amazonian floodplains to date only few have been analysed in more detail in terms of their physiological performance. In single species, respiration, photosynthetic performance and leaf metabolism were analysed, mostly in Master and PhD theses (Piedade 1985; Schlüter 1989; Schlüter and Furch 1992; Schlüter et al. 1993; Maia 1997; Parolin 1997; Waldhoff et al. 1998, 2002; Armbrüster 1999; Graffmann 2000; Horna 2001; Ferreira 2002; Müller 2002; De Simone 2003; Farias 2007). In other studies single physiological aspects were picked out, like leaf chlorophyll contents (Furch 1984) or water potential (Scholander and Perez 1968) of selected species. In these investigations it turned out that the inundation and/or submergence has strong effects on the physiology and growth of the examined tree species.

Among the best analysed species to date are *Astrocaryum jauari* (Arecaceae), *Calophyllum brasiliense* (Clusiaceae), *Cecropia latiloba* (Cecropiaceae), *Crataeva benthamii* (Capparidaceae), *Eschweilera tenuifolia* and *Gustavia augusta* (Lecythidaceae), *Hevea spruceana* (Euphorbiaceae), *Himatanthus sucuuba* and

Tabernaemontana juruana (Apocynaceae), *Laetia corymbulosa* (Flacourtiaceae), *Macrolobium acaciifolium* and *Senna reticulata* (Caesalpiniaceae), *Nectandra amazonum* (Lauraceae), *Pouteria glomerata* (Sapotaceae), *Symmeria paniculata* (Polygonaceae), *Tabebuia barbata* (Bignoniaceae), and *Vitex cymosa* (Verbenaceae).

In the period of low water levels, growth conditions can be extremely favourable, with moist soils and the highest nutrient availabilities among Amazonian ecosystems. However, at the peak of the non-flooded period, drought may play an important role which in combination with cloudless skies and light incidence exceeding 3,000 PAR may cause inhibitions of gas exchange (Long et al. 1994). Other inhibitions occur during the aquatic phase, which occurs in a period in which temperature and light conditions are optimal for plant growth, and thus gas exchange, mainly photosynthesis and transpiration, have to be controlled. None of the species analysed to date show a dormant state over the whole period of flooding – most species reduce their physiological activities only for few weeks (Parolin 2000a) despite hypoxic or even anoxic conditions in the rhizosphere. Oxygen depletion in the root zone is accompanied by increased levels of CO_2, anaerobic decomposition of organic matter, increased solubility of mineral substances, and reduction of the soil redox potential (Joly and Crawford 1982; Kozlowski 1984a,b). The accumulation of many potentially toxic compounds, caused by alterations in the composition of the soil micro flora (Ponnamperuma 1984) are a further consequence. In addition, high sedimentation rates in white-water floodplains (100 mg l^{-1} suspended load in the Amazon River/Rio Solimões; Irion et al. 1997) increase the lack of oxygen in the root zone, and mud layers on the leaf surfaces may affect photosynthesis. The high productivity linked to the high nutrient availability in the várzea (Piedade et al. 1991) results in elevated decomposition rates which further decreases the oxygen levels. In the black water floodplains of the Rio Negro and its affluents (seasonal igapó *sensu* Prance, 1979), additional stress may be caused by the lack of available nutrients (Sioli 1954b; Furch 1997).

However, different tree species developed a high diversity of adaptive strategies which allow them to cope with these problems and permit high photosynthetic activities during most of the year.

10.2 Photosynthesis and Successional Stage

The photosynthetic assimilations measured under natural conditions in Amazonian floodplains lie in the same range as those of other tropical woody plants (Larcher 1994), and this is the case not only in the non-flooded period but in many species also under the extraordinary hydric conditions which annually prevail for many months.

Just as in upland forests (Medina and Klinge 1983; Medina 1984; Oberbauer and Strain 1984; Schulze et al. 1994), Amazon floodplain pioneer species have higher assimilation maxima than non-pioneers, and deciduous trees higher than evergreen species (Parolin et al. 2001). In the pioneers *Cecropia latiloba* and *Senna reticulata* photosynthetic assimilation measured in the field ranged from absoulte minima of 5 to maxima of 28 µmol m^{-2} s^{-1}, whereas the deciduous non-pioneers *Crataeva benthamii*, *Tabebuia barbata* and *Vitex cymosa* had similar minima (3.2–5.4) and lower maxima (15.2–22). The evergreen non-pioneer *Nectandra amazonum* had the lowest minima of maximum CO_2-assimilation A_{max} (3.2 µmol $m^{-2}s^{-1}$) and low maxima (15.6 µmol $m^{-2}s^{-1}$) (Table 10.1).

On the other hand, it is evident that a clear separation of successional groups is not possible. There is more a continuum with fast-growing species like *Alchornea castaneifolia* or *Senna reticulata* on one extreme, performing photosynthetic assimilation of up to 28µmol $m^{-2}s^{-1}$ (Table 10.2). On the other extreme are slow-growing species of late successional stages like *Tabebuia barbata* which have photosynthetic assimilation of maximally 15 µmol $m^{-2}s^{-1}$. In between these

Table 10.1 Average maximum CO_2-assimilation (A_{max}) in the non-flooded terrestrial period (µmol m^{-2} s^{-1}) in adult trees (in the field) and seedlings (under experimental conditions) of the same species. Difference in % (with adult trees = 100%) (After Parolin et al. 2001)

Species	Adults	Seedlings	Difference (%)
Cecropia latiloba	16.8 ± 1.5	10.6 ± 1.4	63.1
Senna reticulata	20.0 ± 4.0	9.2 ± 1.9	46.0
Nectandra amazonum	9.3 ± 2.4	6.7 ± 1.6	72.0
Crataeva benthamii	10.7 ± 4.8	9.0 ± 2.5	84.1
Tabebuia barbata	11.1 ± 2.3	6.3 ± 0.9	56.8
Vitex cymosa	16.6 ± 1.5	8.0 ± 1.1	48.2

Table 10.2 Absolute maxima of CO_2-assimilation (A_{max}) measured in the terrestrial and aquatic phases of the hydrological cycle in selected tree species

	Terrestrial phase	Aquatic phase
Species	A_{max} (µmol m^{-2} s^{-1})	A_{max} (µmol $m^{-2}s^{-1}$)
Alchornea castaenifolia[a]	28	18
Bactris sp.[a]	10	14
Cecropia latiloba[b]	21	18
Crataeva benthamii[a]	10	15
Crataeva benthamii[b]	22	11
Inga sp.[a]	12	20
Nectandra amazonum[a]	10	20
Nectandra amazonum[b]	14	13
Pouteria glomerata[a]	10	15
Psidium acutangulum[a]	7	13
Senna reticulata[b]	25	21
Tabebuia barbata[a]	15	7
Tabebuia barbata[b]	15	13
Vitex cymosa[a]	15	7
Vitex cymosa[b]	20	16

[a] Piedade et al. (2000)

[b] Parolin et al. (2001)

Table 10.3 Quantum yield of the six species in the terrestrial and aquatic phases. Mean quantum yield (mol O_2 per mol quants) and difference between the non-flooded and flooded period in percent (After Parolin et al. 2001)

Species	Successional stage	Mean quantum yield: non-flooded	Mean quantum yield: flooded	Difference (%)
C. latiloba	EP	0.036	0.038	4.5
S. reticulata	EP	0.029	0.030	2.2
N. amazonum	ENP	0.018	0.014	−18.9
C. benthami	DNP	0.049	0.025	−49.3
T. barbata	DNP	0.029	0.018	−39.2
V. cymosa	DNP	0.018	0.011	−35.6

EP, evergreen pioneer; ENP, evergreen non-pioneer; DNP, deciduous non-pioneer

extremes we find the whole range of photosynthetic activities (Table 10.2). The continuum between the extremes is less visible in the flooded period, where differences between the assimilation of pioneers and non-pioneers are more distinct (pioneers 15.0–18.4 μmol $m^{-2} s^{-1}$, non-pioneers 7.6–8.6 μmol $m^{-2} s^{-1}$; Parolin et al. 2001). The same is true for quantum yield and stomatal conductance, where decreases in the flooded period are smaller in pioneer species than in non-pioneers (Table 10.3; Parolin et al. 2001). No such pattern could be found for intercellular CO_2 concentrations and for the ratio of intercellular CO_2 concentrations to CO_2 concentrations in the cuvette (Ci/Ca) (Parolin et al. 2001).

Besides overall growth performance, also the typical leaf characteristics of pioneer trees may be responsible for the differences in photosynthetic performance. The pioneer species, e.g. *Cecropia latiloba* or *Senna reticulata*, have opposite features from sclerophyll species, with high leaf area, leaf dry mass and specific leaf area. Photosynthetic assimilation is highest in the non-sclerophyll pioneers, and lowest in the sclerophyll evergreen non-pioneer *Nectandra amazonum.*

For the efficient establishment of pioneer species, an efficient system of nutrient uptake and high net photosynthetic rates are crucial in order to be able to dominate over the aggressive fast-growing grass vegetation. The assimilation of *Senna reticulata* lies in a range which is normally reached only by highly efficient C3 (e.g. *Eichhornia crassipes*) and C4-herbs (e.g. *Paspalum repens*, *Echinochloa polystachya*) (Larcher 1994; Piedade et al. 1994).

10.3 Photosynthesis and Plant Age

There are no direct comparisons of photosynthetic activities of young and adult plants of the same species in the field. Several studies accompanied photosynthetic activities in the annual cycle in adult trees (Maia 1997; Parolin 1997; Armbrüster 1999), others focussed on seedling performance under experimental semi-natural conditions (Parolin 1997; Waldhoff et al. 1998). The available data are summarized in Table 10.1 (from Parolin et al. 2001): in the six available species, photosynthetic performance of the adult individuals were always very much higher (46–84%) than in individuals of few months age. However it must be kept in mind that seedling data were not gained under optimal field-conditions but from seedlings grown in 2l plastic bags, i.e. reduced root volume, different water regime and light intensities than under natural conditions.

10.4 Photosynthesis and Leaf Age

Leaf age changes from mainly adult leaves at the beginning of flooding, to mainly senescent leaves in the middle of the flooded period and to young leaves towards the end of flooding. In the non-flooded period, adult leaves predominate.

In a study of six tree species (Parolin 1997), a clear positive relationship between photosynthesis and leaf age was found. Although the duration and timing of the leafless period are not directly related to the time of highest water level (Wittmann and Parolin 1999), the production of new leaves occurred primarily in the high water period guaranteeing the presence of fully expanded, adult leaves throughout the non-flooded period. Young or adult leaves had higher photosynthetic activities than senescent leaves. In the months where there was a higher amount of senescent leaves on the trees, mean photosynthetic activity was reduced. Leaf age surely is an explanation for seasonal changes of photosynthesis in the studied species (Parolin 2000b).

10.5 Leaf Photosynthesis in the Annual Cycle

All the studied plants show changes of A_{max} between the terrestrial and the aquatic phase (Piedade et al. 2000). In a long-term study of six common tree species of the várzea with different growth strategies, i.e. typical pioneers and non-pioneers (*sensu* Swaine and Whitmore 1988), and evergreen and deciduous species, the patterns of vegetative phenology and photosynthetic CO_2-assimilation showed characteristic seasonal variations (Fig. 10.1).

10.5.1 The Terrestrial Phase

Photosynthetic CO_2 assimilation at high photon flux density, in the non-flooded terrestrial phase without flooding stress, ranged from a mean of 9.3 μmol $m^{-2} s^{-1}$ for *Nectandra amazonum* (evergreen non-pioneer) to a mean of 20.0 μmol $m^{-2} s^{-1}$ for *Senna reticulata* (evergreen pioneer) (Parolin et al. 2001). This lies well in the range of tropical forests reported in other studies. Early successional rain forest trees have mean photosynthetic assimilation of 8.8–27.7 μmol $m^{-2} s^{-1}$, late successional canopy trees 4.4–11.3 μmol $m^{-2} s^{-1}$ (Bazzaz 1991; Bazzaz and Pickett 1980; Mooney et al. 1980; Oberbauer and Strain 1984).

During the non-flooded phase, periods without rain may cause drought stress in trees (Junk 1997b). In several species, the influence of drought appeared to be by

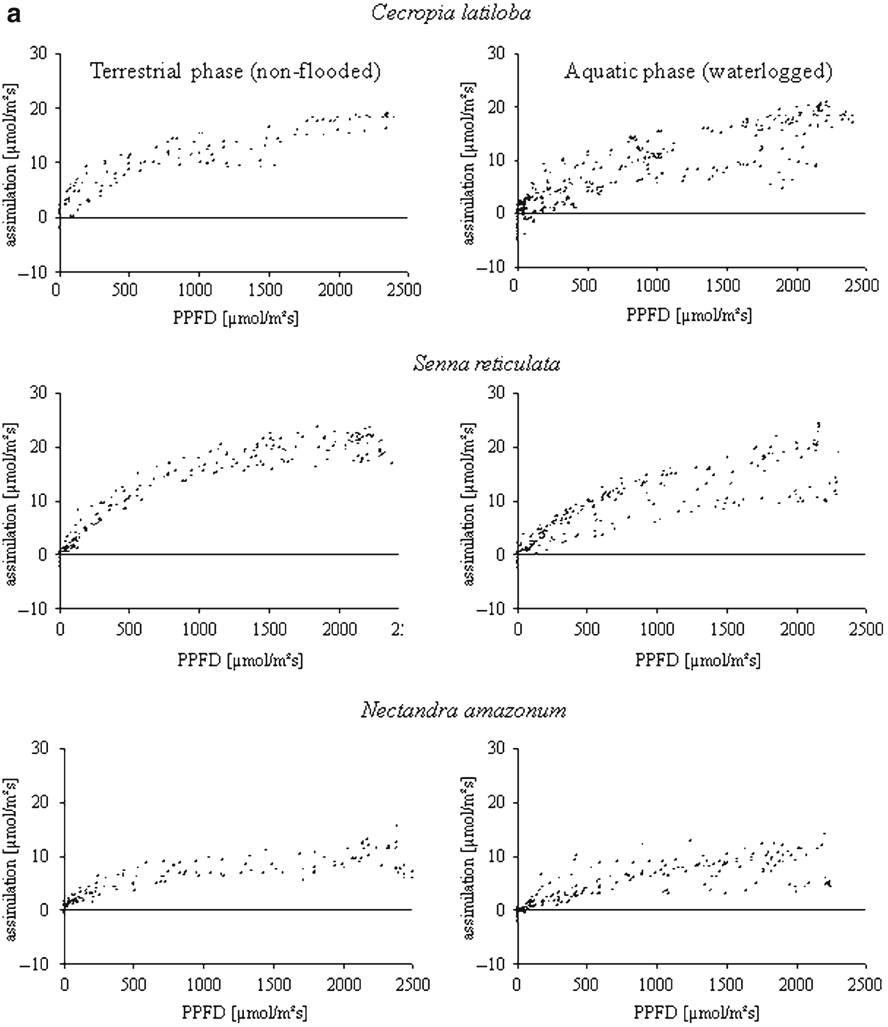

Fig. 10.1 Measured data points during 15 months of recording: photosynthetic assimilation as a function of photon flux density in non-flooded terrestrial and flooded aquatic phase (**a**) in the evergreen pioneer *Cecropia latiloba* and *Senna reticulata*, and the evergreen non-pioneer *Nectrandra amazonum*; (**b**) in the deciduous non-pioneers *Tabebuia barbata* and *Vitex cymosa*

far more harmful than that of waterlogging or even submergence in terms of growth, photosynthetic performance and vitality after stress end (Waldhoff et al. 1998). In fact, drought may represent more of an impairment to survival than flooding to the local vegetation (Keel and Prance 1979; Scarano et al. 1994). Waldhoff et al. (1998) found photosynthetic assimilation of about 4 µmol $m^{-2} s^{-1}$ in *Pseudobombax munguba* as response to drought, where waterlogged seedlings showed 8 µmol $m^{-2} s^{-1}$ and the control plants 12.5 µmol $m^{-2} s^{-1}$.

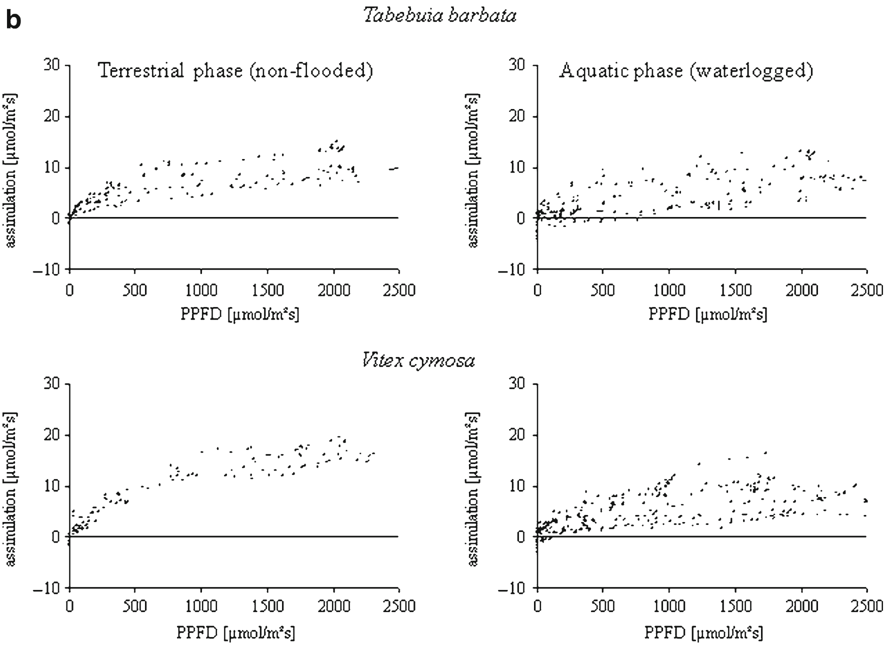

Fig. 10.1 (continued)

10.5.2 The Aquatic Phase

Many trees perform the highest absolute values of CO_2 assimilation in the aquatic phase (Parolin 2000a, Table 10.2), although overall means are higher in the non-flooded period in most species (Table 10.4). In fact, in the flooded period many trees show reduced mean photosynthetic assimilations in aerial leaves which range from 10% (early successional *Cecropia latiloba*, *Senna reticulata*) to 20–50% (late successional *Nectandra amazonum*, *Crataeva benthamii*, *Tabebuia barbata*, *Vitex cymosa*) lower CO_2-uptake than in the terrestrial phase (Parolin et al. 2001; Piedade et al. 2000).

After the beginning of flooding, CO_2-uptake is high in the first months of flooding, and is reduced after some months. In the second part of the aquatic phase, CO_2-uptake rises again to levels which are comparable to those of the terrestrial phase, or even more elevated. This takes place before the end of flooding in all species (Parolin 2000a).

Waterlogged adults or seedlings of *Senna reticulata* often showed higher assimilation rates than non-flooded individuals: in a flooding experiment, waterlogged seedlings had an average assimilation rate which was 15% higher than that of the well-watered control (Parolin 2001a). *Senna reticulata*, flooded by a water column of 4 m with only few leaves appearing above the water surface showed assimilation rates of up to 25 µmol CO_2 $m^{-2} s^{-1}$, which represent the highest photosynthetic activity measured in waterlogged Amazonian floodplain trees (Parolin 2001a).

Table 10.4 Mean CO_2 assimilation (μmol CO_2 m^{-2} s^{-1}) and standard deviation in the terrestrial and aquatic phases, differences in percent (non-flooded period = 100%), ANOVA F-ratio and probability p. n = 80 (After Parolin et al. 2001)

Species	Mean CO_2 assimilation: non-flooded	Mean CO_2 assimilation: flooded	Difference (%)	F-ratio	p
Cecropia latiloba	16.8 ± 1.5	15.0 ± 4.6	−10.5	2.21	n.s.
Senna reticulata	20.0 ± 4.0	18.4 ± 4.3	−7.8	18.07	***
Nectandra amazonum	9.3 ± 2.4	7.6 ± 3.1	−18.7	6.36	*
Crataeva benthamii	10.7 ± 4.8	8.6 ± 1.0	−19.7	6.02	*
Tabebuia barbata	11.1 ± 2.3	8.6 ± 2.6	−21.9	13.38	**
Vitex cymosa	16.6 ± 1.5	8.4 ± 2.2	−49.2	161.05	***

Two main factors can be responsible for the reductions of mean photosynthetic values over the flooded period. Photosynthetic capacity itself can be affected, or stomatal effects can cause changes in CO_2-assimilation. Since in six analysed species stomatal conductances increased in the flooded period, this factor cannot be limiting for photosynthesis and does not seem to be responsible for the decrease of assimilation. This is reflected also by the generally higher intercellular CO_2 concentrations in the flooded period (Parolin et al. 2001), which then cannot be limiting photosynthesis.

In seedlings of the same analysed species, reduction of assimilation was closely related to the reduction of stomatal conductivity. However, with waterlogging assimilation sank only in four species, by −25% to −100%. The seedlings of *Senna reticulata* and *Nectandra amazonum* had 15–22% higher assimilations with waterlogging than in control. This so far has been observed only in few very flood-tolerant grasses (Rubio et al. 1995), herbs (Whiteman et al. 1984) and some trees like *Hymenaea courbaril* and *Chorisia speciosa* (Joly and Crawford 1982). All in all it appears that in central Amazonian floodplains many tree species have their highest photosynthetic activity in the aquatic phase (Piedade et al. 2000).

10.6 Chlorophyll Fluorescence in Submerged Leaves

Chlorophyll *a* fluorescence ('current photochemical capacity' of photosystem II; PSII) measurements indicate similar trends as the measurements of photosynthetic assimilation performed with infra-red gas analyzers mentioned above. The ratio of Fv/Fm is the photochemical efficiency which is a measure for the stress condition of a plant (Seaton and Walker 1992). The stronger a disturbance, the more the quotient Fv/Fm decreases. In six analysed tree species the typical Fv/Fm value of non-stressed leaves lay between 0.73 and 0.76 (Table 10.5, Parolin 1997). Three species showed a reduction of Fv/Fm in the aquatic period when compared to the terrestrial period, others did not show clear differences. In the terrestrial period, Fv/Fm of *Nectandra amazonum* was 0.75, in the aquatic period the ratio sank significantly by 5.0% to below 0.7. The highest reductions of Fv/Fm were measured in *Tabebuia barbata*, where the ratio sank by 4.8% in the flooded period as compared to the non-flooded one.

Table 10.5 Photochemical efficiency (Fv/Fm) of six tree species in the terrestrial and aquatic phase (from Parolin 1997). Lowest and highest measured values (min–max), means with standard deviation, difference between terrestrial and aquatic phase in percent. Significance calculated with F-ratio ANOVA and statistical probability P; sample size n = 60. *Vitex cymosa* was measured only in the aquatic period

Species	min–max	Terrestrial phase	Aquatic phase	Difference (%)	F-ratio	p
C. latiloba	0.51–0.80	0.65 ± 0.0	0.68 ± 0.1	3.0	1.37	n.s.
S. reticulata	0.59–0.84	0.74 ± 0.1	0.73 ± 0.0	−1.3	1.69	n.s.
N. amazonum	0.57–0.82	0.73 ± 0.0	0.70 ± 0.1	−5.0	5.34	*
C. benthami	0.68–0.81	0.75 ± 0.0	0.79 ± 0.0	4.1	0.49	n.s.
T. barbata	0.61–0.82	0.76 ± 0.0	0.72 ± 0.0	−4.8	11.79	***
V. cymosa			0.72 ± 0.1			

An interesting factor is the "threshold value of impairment" ("Störungsschwellenwert", Bolhár-Nordenkampf and Götzl 1992; Waldhoff et al. 2002) which in European trees – where the method was developed – has a critical limit at a Fv/Fm of 0.72. It is the lowest level of the natural variation of fluorescence. In Amazonian floodplain trees, most mean values of are a priori below this limit. Only in *Senna reticulata* the mean ratio was higher than this threshold value, although single measurements of non-stressed plants showed Fv/Fm around 0.59 (Parolin 1997).

Waldhoff et al (2002) analysed *Symmeria paniculata*, a common evergreen tree species from the lowest part of the flooding gradient in black-water inundation forests in central Amazonia which does not shed submerged leaves. Chlorophyll a fluorescence was measured regularly in non-submerged and submerged leaves of different age classes, and measurements at up to 8 m under the water were performed. The Fv/Fm values in non-submerged leaves and in those submerged at 0–1 m depth were not correlated with the changing water levels and remained above the lower limit of natural variation of healthy leaves (>0.66), indicating an undamaged photochemical apparatus. Younger leaves showed higher Fv/Fm values than older leaves which in turn showed higher values than in currently submerged leaves. Leaves submerged in darkness (1–7 m depth, up to 163 days of submergence at the time of measuring) showed Fv/Fm values between 0.7 and 0.4, and were negatively correlated with the duration of submergence. The recovery of these Fv/Fm values to mostly >0.7 during falling water levels apparently took place when still underwater. 'Rapid light curves' of leaves submerged at >1 m depth revealed that the PSII started with electron transport when illuminated. However, the electron transport was apparently inhibited shortly after the start. A negative correlation was found between the inhibition of electron transport and the depth/duration of submergence.

Submerged leaves maintained their vitality despite almost complete darkness below water: even at water depths of 1–7 m, with a quantum flux of 1–10 µmol m^{-2} s^{-1} (PAR), Fv/Fm values lay below this threshold, showing a negative correlation with the duration of submergence (Waldhoff et al. 2002). The fact that the current photochemical capacity of the seedlings' leaves of different species (e.g. *Nectandra amazonum*, *Tabernaemontana juruana*, *Gustavia augusta*, Waldhoff et al. 2000) submerged in the dark declined to almost zero and recovered within 10 days to values in the range of healthy and well-functioning leaves (undamaged PSII), clearly demonstrates strong adaptation to the half-a-year inundation of the várzea floodplains. The energy needed for the recovery of leaves flooded in the dark is so low that it is more advantageous to maintain some leaves rather than to shed them all. Two strategies may be postulated (Junk pers. comm.) to cope with this problem, which both are highly efficient. Trees which maintain their leaves below water can maintain photosynthesic activities also below water, but these are low-light plants (e.g. *Symmeria paniculata*). Those species, which shed all the leaves with flooding, have a shorter time for photosynthesis, but they make the maximum out of this short period because they are high-light plants.

Several species (e.g. *Nectandra amazonum, Gustavia augusta*, and *Tabernaemontana juruana*) maintain their photosynthetic apparatus at least so far undamaged that seedlings can start to photosynthesize shortly after emergence (Parolin 1997; Waldhoff et al. 2000). In *Tabernaemontana juruana*, light saturation before submersion (800 μmol m^{-2} s^{-1}) did not differ much from the values after submersion (500 μmol m^{-2} s^{-1}; Krack 2000). Within 3 weeks of exposure, pre-flood values were achieved. In *Laetia corymbulosa* and *Tabernaemontana juruana*, light harvesting was even higher after recovery than before submersion (Krack 2000).

The main problem the leaves probably have to deal with after the end of flooding is the light rather than the presence or absence of water. The question about the mechanisms that maintain the photosynthetic apparatus almost undamaged during the submersion is still open. Leaves of adult trees that were submerged in darkness (>1m depth) recovered the Fv/Fm-yield while still under water, during falling water levels, independently of how long the leaves were submerged prior to the measurements. There is a correlation between light intensity and the maintenance/recovery of the photosynthetic apparatus (PSII).

In a greenhouse experiment, the light harvesting complex of submerged seedlings of *Tabernaemontana juruana, Pouteria glomerata, Laetia corymbulosa, Gustavia augusta*, and *Nectandra amazonum* did not deteriorate, Rubisco was decomposed only to a low extent, and new proteins with unknown function were synthesized and accumulated during submergence (Krack 2000). The same seedlings survived submergence only if they were well supplied with nutrients before flooding and if they were at least 5 months old (Krack 2000), indicating that these processes imply high energy costs. Nevertheless, the energy balance in submerged seedlings is highly effective: in the palm *Astrocaryum jauari*, the energy reserves in the roots were not exhausted after 300 days of submersion (Schlüter et al. 1993).

10.7 Transpiration

CO_2-assimilation and transpiration are coupled over the stomata. Accordingly, the annual changes of these two parameters are mostly similar. The transpiration values lay on the average between 4,000 and 8,000 μmol m^{-2} s^{-1} (Table 10.8). The highest values were measured in the pioneer species and the lowest in evergreen non-pioneers like *Nectandra amazonum*. Most species (but not *Tabebuia barbata*) had lower transpiration in the aquatic phase than in the terrestrial phase (by up to 30%). Lowest transpiration occurred in the period between June and August, approximately at highest river levels. Shortly before the end of the waterlogged period, in the analysed trees of several species transpiration rose to its maximum (nearly 7,000 μmol $m^{-2} s^{-1}$), at the same time of maximum leaf flush, and sank again in the middle of the terrestrial phase. More information on transpiration is given in Chapter 11 (Horna et al. 2010).

10.8 Stomatal Conductance, Intercellular CO_2 Concentrations Ci and Ci/Ca

Mean stomatal conductance for CO_2 (gs) indicates the degree of opening of the stomata (Buschmann and Grumbach 1985). In six analysed species, it ranged between 200 and 400 mmol m^{-2} s^{-1} (Parolin 1997), *Tabebuia barbata* having the lowest and *Senna reticulata* the highest gs (Table 10.6). It increased between 5% and 35% in all species when flooded (Table 10.6).

In the annual cycle, the changes in stomatal conductance were sometimes contrary to the changes of maximum CO_2-assimilation and transpiration. In the months in which *Cecropia latiloba* and *Senna reticulata* (both evergreen pioneers), *Nectandra amazonum* (evergreen non-pioneer) and *Crataeva benthamii* (deciduous non-pioneer) had their oldest leaves and lowest CO_2-assimilation – at the end of the aquatic period – stomatal conductance was highest.

During the entire period of data recording, *Cecropia latiloba* showed stomatal conductances between 200 and 450 mmol m^{-2} s^{-1}, in July however they rose to nearly 700 mmol m^{-2} s^{-1}. The differences between terrestrial and aquatic phase were statistically not significant ($p = 0.148$). In *Senna reticulata* there was a reduction of the gs (not significant, $p = 0.481$) with beginning of the terrestrial phase, which were otherwise constant at 400 mmol m^{-2} s^{-1}. Likewise in July,

Table 10.6 Stomatal conductance of six tree species in the terrestrial and aquatic phase (from Parolin 1997). Lowest and highest measured values (min–max), means with standard deviation, difference between terrestrial and aquatic phase in percent. Significance calculated with F-ratio ANOVA and statistical probability P; sample size n = 80 (After Parolin et al. 2001)

Species	Min–max (mmol m^{-2} s^{-1})	Terrestrial phase (mmol m^{-2} s^{-1})	Aquatic phase (mmol m^{-2} s^{-1})	Difference (%)	F-ratio	p
C. latiloba	136–693	333.1 ± 65	382.0 ± 128	14.7	2.13	n.s.
S. reticulata	181–712	402.4 ± 81	422.3 ± 137	5.0	0.50	n.s.
N. amazonum	81–493	209.7 ± 105	225.0 ± 114	7.3	0.29	n.s.
C. benthami	69–645	232.5 ± 132	314.4 ± 105	35.2	6.40	*
T. barbata	60–418	186.1 ± 66	222.9 ± 104	19.8	2.27	n.s.
V. cymosa	104–546	288.7 ± 56	288.5 ± 121	−0.1	0	n.s.

Table 10.7 Summary of gas exchange responses: ratio of intercellular CO_2 concentrations to CO_2 concentrations in the cuvette (Ci/Ca), and calculated intercellular CO_2 concentrations. Means, standard deviation and difference between the non-flooded and flooded period in percent. n = 80 (After Parolin et al. 2001)

	Ci/Ca			Ci (µmol mol^{-1})		
Species	Non-flooded	Flooded	Diff. (%)	Non-flooded	Flooded	Diff. (%)
C. latiloba	0.66 ± 0.02	0.69 ± 0.09	4.5	272 ± 27	262 ± 34	−3.7
S. reticulata	0.61 ± 0.07	0.67 ± 0.07	9.8	231 ± 34	253 ± 29	9.5
N. amazonum	0.71 ± 0.06	0.77 ± 0.07	8.5	281 ± 40	284 ± 24	1.1
C. benthami	0.67 ± 0.12	0.65 ± 0.18	−2.9	259 ± 42	240 ± 60	−7.3
T. barbata	0.62 ± 0.10	0.74 ± 0.05	19.4	240 ± 39	278 ± 21	15.8
V. cymosa	0.60 ± 0.01	0.79 ± 0.07	31.7	230 ± 7	302 ± 26	31.3

Nectandra amazonum had the highest gs (average value with 400 mmol $m^{-2} s^{-1}$). They first sank during the terrestrial phase to below 100 mmol $m^{-2} s^{-1}$, and then rose again to 350 mmol $m^{-2} s^{-1}$.

Also in *Crataeva benthamii* very high gs (600 mmol $m^{-2} s^{-1}$) were measured shortly before leaf shedding, in June and July, which then sank under 100 mmol $m^{-2} s^{-1}$ from September on. They rose again only to end of the terrestrial phase ($p = 0.014$). *Tabebuia barbata* had the highest values in the first month of the aquatic phase, afterwards they sank again ($p = 0.137$). Also at the beginning of the terrestrial phase, gs was relatively high and sank continuously thereafter. In the middle of the aquatic phase *Vitex cymosa* had the highest stomatal conductivity. Afterwards gs sank, rose slightly in the terrestrial phase and sank again with the beginning of the aquatic phase ($p = 0.995$).

Calculated mean intercellular CO_2 concentrations (Ci) increased with flooding in some species, not so in others, e.g. *Cecropia latiloba* (evergreen pioneer) and *Crataeva benthamii* (deciduous non-pioneer) (Table 10.7).

Mean ratio of intercellular CO_2 concentrations to CO_2 concentrations in the cuvette (Ci/Ca) increased with flooding in all species (Table 10.7).

The reduction of photosynthesis with waterlogging is frequently caused by partial closure of the stomata (Zaerr 1983; Larcher 1994). In the analysed six species, only in *Senna reticulata* there was a statistically significant relation between changes of assimilation and stomatal conductivity, which point to the closure of the stomata (Table 10.8).

10.9 Leaf Chlorophyll Content

Leaf chlorophyll content is an important parameter for the physiological condition of the leaves and for photosynthetic activity, since it is limiting for the photosynthetic CO_2 fixation (Medina and Lieth 1964). The measured chlorophyll

Table 10.8 Transpiration of six tree species in the terrestrial and aquatic phase: lowest and highest measured values (min–max), average values, standard deviation, difference between terrestrial and aquatic phase in %. F-values of the ANOVA and statistic probability p are presented; sample size (n) = 80

Species	Min–max (%)	Terrestrial phase (%)	Aquatic phase (%)	Difference (%)	F-ratio	p
C. latiloba	1,074–9,590	8,231 ± 1,244	5,702 ± 2,609	−30.7	13.89	***
S. reticulata	6,156–9,895	7,850 ± 663	7,647 ± 943	−2.6	0.94	n.s.
N. amazonum	829–6,853	5,205 ± 896	3,900 ± 2,082	−25.1	11.51	***
C. benthami	1,000–10,563	6,157 ± 2,456	4,026 ± 2,754	−34.6	12.46	***
T. barbata	2,353–8,372	5,117 ± 1,014	6,004 ± 1,513	17.3	6.09	*
V. cymosa	551–8,817	7,661 ± 479	5,257 ± 2,597	−31.4	11.51	***

contents per leaf area of aerial leaves of several species are in the range of 142% (*Vitex cymosa*) to 737% (*Tabebuia barbata*) (Table 10.9). Seedlings of several analysed species showed lower chlorophyll contents than adults (Parolin 1997).

10.9.1 Leaf Chlorophyll Content with Flooding

With waterlogging, chlorophyll content of aerial leaves is lower than without flooding (Scholander and Perez 1968; Furch 1984; Schlüter and Furch 1992; Schlüter et al. 1993; Parolin 1997; Waldhoff et al. 1998), as was shown for six analysed tree species (Table 10.9). The overall water supply and availability are an important factor for leaf chlorophyll contents (Kyparissis et al. 1995). In fact most species (not so in *Vitex cymosa*) showed a close correlation between changes of chlorophyll content and changes of leaf water content and/or water potential, in the annual cycle.

On the other hand, leaf chlorophyll content is also linked to leaf age: with the aging of the leaves chlorophyll is resorbed (Sestak 1985). In adult leaves, reductions of chlorophyll content are caused by lack of nutrients, pathogens or senescence, and waterlogging (Medina and Lieth 1964; Parolin 1997). An increase of chlorophyll contents under waterlogged conditions, as it was measured in seedlings of *Senna reticulata*, may be related to the strong production of adventitious roots and the resulting enhanced water supply (Parolin 1997).

In some species which do not shed leaves below water, e.g. *Symmeria paniculata*, *Tabernaemontana juruana*, and *Gustavia augusta*, chlorophyll content was little affected in the submerged leaves (Waldhoff et al. 1998, 2002).

10.9.2 Relationship of Chlorophyll a:b

The relationship of chlorophyll a:b describes which photosynthetic achievements a plant can potentially accomplish (Sestak 1985). The values of the relationship of chlorophyll a:b of six analysed species lay between 2.7 and 4.4 (Table 10.10). The lowest relationship of chlorophyll a:b was found in *Tabebuia barbata*, the highest in *Cecropia latiloba*. Only two kinds had an increase of the relationship from the terrestrial to the aquatic phase (*Cecropia latiloba* and *Vitex cymosa*), while it decreased in most other species.

In submerged leaves, Chl a:b was below 3. Investigations of Furch (1984) in submerged leaves of 21 tree species from Amazonian floodplain forests showed a higher content of chlorophyll b due to the lack of light, with unchanged content of chlorophyll a. Thus the relationship Chl a:b sinks, reaching values which are comparable to macrophytes living under water (3.7–1.8).

With waterlogging of the roots, Chl a:b of the non-submerged leaves of most species sank significantly. This is astonishing since in the aquatic phase light

Table 10.9 Chlorophyll content per leaf area of six tree species in the terrestrial and aquatic phase: lowest and highest measured values (min–max), average values, standard deviation, difference between terrestrial and aquatic phase in %. F-values of the ANOVA and statistic probability p are presented; sample size (n) = 30

Species	Min–max (%)	Terrestrial phase (%)	Aquatic phase (%)	Difference (%)	F-ratio	p
C. latiloba	301–715	527.3 ± 277	442.9 ± 69	−16.0	4.55	*
S. reticulata	309–563	430.7 ± 67	444.6 ± 53	3.2	0.29	n.s.
N. amazonum	150–628	269.5 ± 55	467.3 ± 85	73.4	50.98	***
C. benthami	205–706	556.3 ± 93	416.8 ± 121	−25.1	10.13	**
T. barbata	193–737	573.3 ± 91	284.4 ± 64	−50.4	81.14	***
V. cymosa	142–625	526.3 ± 63	305.6 ± 96	−41.9	32.94	***

Table 10.10 Relationship of chlorophyll a:b in six tree species in the terrestrial and aquatic phase: lowest and highest measured values (min–max), average values, standard deviation, difference between terrestrial and aquatic phase in %. F-values of the ANOVA and statistic probability p are presented; sample size (n) = 15

Species	Min–max (%)	Terrestrial phase (%)	Aquatic phase (%)	Difference (%)	F-ratio	p
C. latiloba	3.1–7.1	3.6 ± 0.4	4.4 ± 1.3	21.0	1.20	n.s.
S. reticulata	3.3–4.7	4.1 ± 0.2	3.4 ± 0.9	−16.6	3.41	n.s.
N. amazonum	2.1–5.4	3.9 ± 0.6	3.7 ± 0.7	−5.5	0.31	n.s.
C. benthami	1.9–4.4	4.0 ± 0.3	3.5 ± 0.1	−12.9	12.24	**
T. barbata	2.1–3.8	3.4 ± 0.3	2.7 ± 0.6	−21.4	6.89	*
V. cymosa	1.8–5.3	3.3 ± 0.4	3.5 ± 0.9	4.0	0.07	n.s.

incidence is higher because of the reflectance on the water surface and because many trees are without leaves. Thus a shift of the relationship was expected in favor of Chl a. Perhaps an explanation stands in connection with the aging of the leaves (Sestak 1985) which is pronounced in the waterlogged months.

10.10 Leaf Nitrogen Content

The quantity of nutrients per leaf unit area or leaf weight is a measure of the costs of the structure of the photosynthetic surface (Medina 1984). Leaf nitrogen content is a relatively uniform parameter among different leaf types (1–4 g m^{-2}) (Schulze et al. 1994). In the analysed species, in the terrestrial phase, pioneer trees had the highest leaf nitrogen contents, followed by the deciduous non-pioneers and the evergreen non-pioneers. Most values lie in ranges which were measured also for other tropical woody species (Medina 1984), varying between 1.3% and 3.2% in the terrestrial phase (Table 10.11, Parolin et al. 2002c). The deciduous species, as expected (Medina 1984), had leaves with higher leaf nitrogen contents than evergreen species. In *Nectandra amazonum*, the lowest nitrogen contents were measured, the highest were found in *Senna reticulata* (3.7%).

Many species had lower leaf nitrogen contents in the aquatic phase than in the terrestrial phase (Table 10.11). When not flooded, leaf nitrogen contents went back over up to a quarter. However, waterlogged *Nectandra amazonum* showed an increase of about a third in relation to the terrestrial phase. With flood end, some species showed increased nitrogen content even without flushing new leaves (Fig. 10.2a, e, f). These peaks measured in October may be related to the fact that most plants respond to increased nitrogen availability with significant increases in leaf nitrogen content (Osman and Milthorpe 1971). With the end of submergence, the roots recover their normal functioning (Meyer 1991) and the increased nitrogen uptake is reflected by higher leaf nitrogen values.

New leaves flushed at high water levels often showed high nitrogen contents. This does not result from an increased uptake of nitrogen, but from the internal cycling of

Table 10.11 Mean leaf nitrogen content of different species in the non-flooded and waterlogged months: minimum and maximum measured nitrogen contents, average of the measurements in the terrestrial phase, average of the measurements in the aquatic phase with standard deviations, difference between terrestrial (= 100%) and aquatic phase, F-ratio ANOVA and statistical probability p (After Parolin et al. 2002)

Species	Min–max (%)	Terrestrial phase (%)	Aquatic phase (%)	Difference (%)	F-ratio	p
C. latiloba	2.1–3.6	2.6 ± 0.4	2.5 ± 0.4	−2.5	0.27	n.s.
S. reticulata	2.0–3.7	3.2 ± 0.5	2.5 ± 0.2	−21.1	23.83	***
N. amazonum	1.0–2.2	1.3 ± 0.2	1.7 ± 0.4	31.6	14.43	***
C. benthami	1.4–3.4	2.6 ± 0.5	2.4 ± 0.6	−8.1	1.18	n.s.
T. barbata	0.9–2.4	1.9 ± 0.2	1.5 ± 0.5	−19.7	5.99	*
V. cymosa	0.8–2.6	1.9 ± 0.4	1.4 ± 0.3	−24.6	17.36	***

*$p \geq 0.05$; **$p \geq 0.01$; ***$p \geq 0.001$; n.s. not significant

stored reserves (Millard and Proe 1991). A key process in such internal cycling is the withdrawal of nitrogen from leaves during senescence for storage in shoots and roots (May and Killingbeck 1992). In fact, nitrogen content is highest in newly developed young leaves and decreases with leaf age (Field and Mooney 1983).

10.11 Discussion

Several hundred tree species with differing growth strategies manage to adapt to the extreme conditions of Amazonian floodplains. There is no dominance of specific strategies, but a high diversity of species and strategies which coexist and are all efficient against flooding stress. In fact, in many species studied so far, A_{max} was higher in the aquatic phase than in the terrestrial period, particularly when new leaves were flushed. In this case, leaf phenology appears to be an important factor (Piedade et al. 2000). But phenology alone does not explain the results, as shown by *Tabebuia barbata* and *Crataeva benthamii*, two deciduous species. They showed opposite responses with respect to leaf age and photosynthetic activity versus hydroperiod.

The light demand of each group of species (Waldhoff et al. 1998) and climatic conditions, such as temperature and radiation, may play an important role, since they interfere in the hydric balance of the plant and, consequently, in the photosynthesis during contrasting periods of the hydrological cycle.

Endogenous cycles are possibly promoting different inabilities to perform higher leaf CO_2 assimilation rates during the flood. Those endogeneous cycles, on the other hand, are possibly related to the fact that these species originate from semi-deciduous forests and savannas (Kubitzki 1989a,b,c) and represent pre-adaptations which allowed the trees to immigrate into the floodplains.

It seems that plants that are maximising assimilation rates of CO_2 during the terrestrial phase might be less adapted to flooding than those that flush new leaves

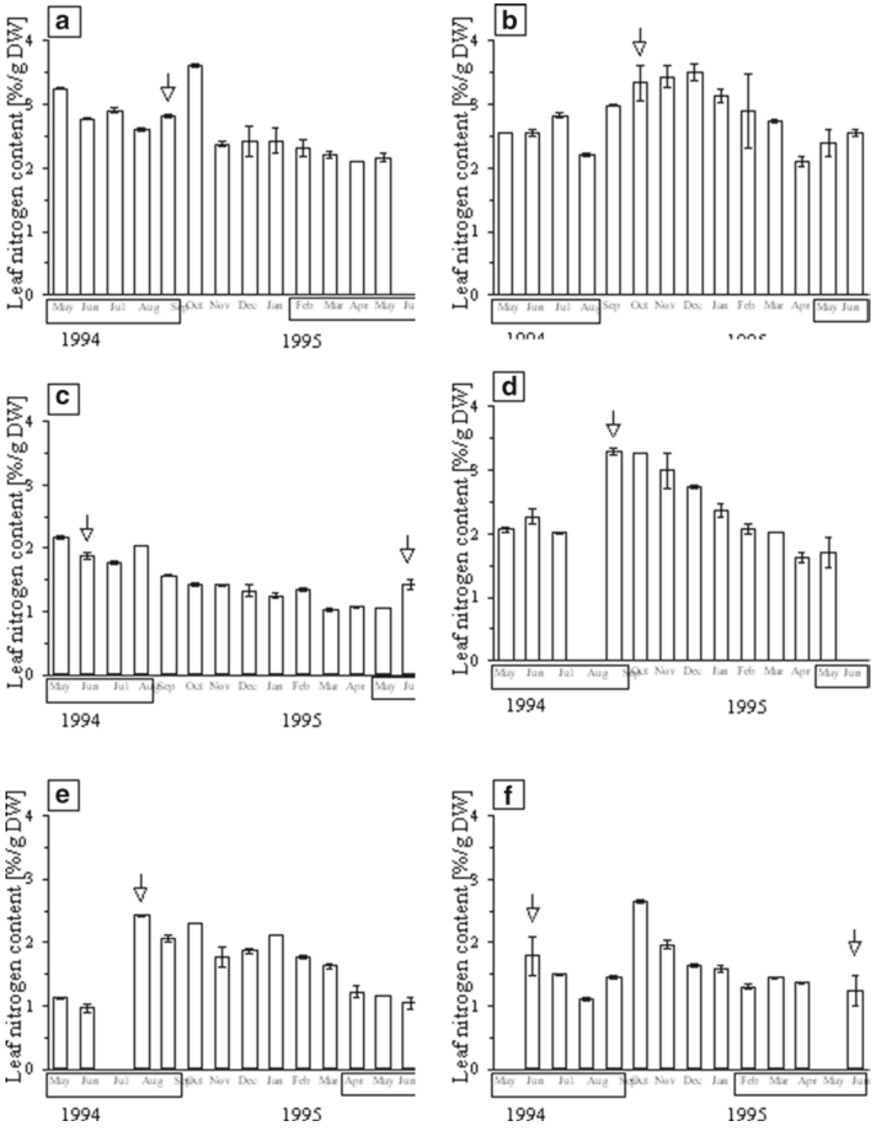

Fig. 10.2 Leaf nitrogen content in the annual cycle of (**a**) *Cecropia latiloba*, (**b**) *Senna reticulata*, (**c**) *Nectandra amazonum*, (**d**) *Crataeva benthamii*, (**e**) *Tabebuia barbata*, and (**f**) *Vitex cymosa*. Monthly nitrogen content as percent of leaf dry weight, with standard deviation, between May 1994 and June 1995. Sample size per species and month (n) = 3 measurements of combined samples from 5 trees. Months in box = aquatic phase. Arrow = flush of new leaves (From Parolin et al. 2002)

when flooded and have higher photosynthetic activity in the aquatic period (Piedade et al. 2000). However, for more conclusive analyses of trends, medium values of A_{max} in the aquatic and terrestrial phases should be analysed in more details, under the same theoretical approach.

Piedade et al. (2000) monitored maximum leaf CO_2 assimilation (A_{max}) and phenology along the hydrological cycle for nine common species, identifying two groups: I – trees maximising A and changing leaves during the aquatic phase (six species); II – trees declining A_{max} during the aquatic phase (three species). Reduction in A_{max} was modest in a few weeks of inundation, and was reduced further in time, eventually approaching zero. The adaptation to the flood pulse in relation to physiological parameters and time of colonisation is discussed.

As in some aquatic grasses (Crawford 1992), trees in the Amazon floodplain could accumulate sugars for use during flooding. *Tabebuia barbata* has more sugars in the stem bark during the aquatic phase than *Crataeva benthamii*. This could explain why the former species showed lower A_{max}: *Tabebuia barbata* can apparently take advantage of a greater sugar supply already stored.

Summarizing, like in other wetland species (Insausti et al.), flooding in many Amazonian floodplain species enhances stomatal conductance, leaf water potential and net photosynthesis, especially under conditions leading to high air-vapour pressure deficits. Therefore, tight regulation of water and carbon relations under severe soil-oxygen deficiencies may give these species the dominance over natural competitors which may be more efficient under non-flooded conditions but are unable to compete when inundated. The different adaptive responses might help to explain the observed diversity of species and the abundance of single species on determined levels along the flooding gradient.

Chapter 11
Sap Flow and Stem Respiration

Viviana Horna, Reiner Zimmermann, Ewald Müller, and Pia Parolin

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Abstract The effects of seasonal flooding on stem xylem flow and carbon release were investigated on common tree species of the Amazonian floodplain forests locally known as Várzea. The annual flooding lasts several months, reaches five to eight meters and drives the phenology of most forest species. Leaf shedding of deciduous trees starts at the onset of flooding and new leaves are produced after

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the peak of flooding in July. For evergreen species leaf shedding and new leaf production occur simultaneously during flooding. It has been generally assumed that these phenology patterns are associated to physiological stress during flooding. Here the focus is on tree and species functioning during water stress by flooding. Measurements of stem xylem flux and stem carbon release were taken to monitor changes in species ecophysiological behavior during flooding.

Transpiration of deciduous trees was high and not significantly reduced by the onset of flooding as long as the main foliage was present. In contrast evergreen species had through all seasons constant sap flux rates. In comparison to other studies in tropical and temperate trees, the conductive area estimated for várzea trees is considerably smaller. As a consequence estimated annual stand transpiration was relatively low (283.5 mm).

Regarding carbon release, it was confirmed that variation in CO_2 release is associated with variation in flooding. Stem- CO_2 emission did not follow changes in leaf phenology but higher stem carbon release was clearly associated higher flooding. The results of this study provide evidence of tree functioning under high metabolic demand due to ambient stress caused by flooding. Future research should focus on the seasonal pattern of carbon allocation and partitioning in várzea trees in relation to species and phenological pattern.

11.1 Introduction

The annual flooding of várzea ecosystems results in phenological, morphological and physiological responses of tree species (Worbes 1997; Schlüter 1989; Schlüter and Furch 1992; Parolin 1997; Waldhoff et al. 1998). Anaerobic conditions cause a decrease in root activity and induce cambial dormancy (Worbes 1997; Schöngart et al. 2002) and leaf fall in várzea tree species (Ayres 1993; Parolin 1997; Wittmann and Parolin 1999). An open question is whether the loss of foliage during inundation is a function of water stress caused by restricted root water uptake – which should lead to a drastic decrease in pre-leaf shedding transpiration – or whether it is a function of a phenological cycle which coincides with the inundation period. The second hypothesis is supported by the observation that new leaves of most species are produced several weeks before the end of the inundation period (Schöngart et al. 2002). The underlying question is whether the observed decrease in leaf transpiration with rising water level (Parolin 1997) is related to an internal fixed phenological cycle or is a function of restricted water uptake and transport during the inundation period. The latter being a consequence of lack of energy supply to anaerobic root tissue (Kozlowski 1997).

Only few publications concerning water relations of tropical trees in the Amazon region have appeared in the last 2 decades, e.g. Shuttleworth et al. (1984), Roberts et al. (1990), Machado and Tyree (1994), Oren et al. (1996), Parolin et al. (2005), and Dünisch and Morais (2002). Only the study of Parolin et al. (2005) deals with the effects of flooding in Amazonian várzea. Parolin compared the transpiration of single leaves of six várzea tree species during a complete annual cycle. A first indication of a distinct reduction of transpiration during the inundation phase was found, but also different reactions between the observed species were revealed, bringing attention to the scarce knowledge available about the strategies of várzea trees to survive soil waterlogging.

In this chapter, we compare data on the annual cycle of water transport and stem carbon release of várzea trees with contrasting phenology patterns. We aim to determine for different phenological types, the rates of apparent stem water uptake and stem carbon release activity during flooding and non-flooding conditions. Additionally, we discuss the variation in hydroactive sapwood area in várzea trees and compare it to the sapwood area of other tropical and temperate tree species. The amount of available sapwood area is important to determine the total flux of water per tree. The objective of this chapter is to give an overview of the ecophysiological functioning of várzea tree stems with focus on the seasonality of water transport and carbon release and their seasonal variation in várzea forests.

The data presented here combines two studies carried out within a large cooperation project to conduct research on the ecology of tropical forest floodplains (SHIFT). The first study focused on the detailed evaluation of water uptake and the determination of sapwood area from six tree species common to the várzea forest (Parolin et al. 2005). The second study extended on the evaluation of stem carbon release from eight várzea tree species including the six species monitored by Parolin et al. (2005) and continued parallel measurements of water uptake on nine tree species (Horna 2002). Because of the setup and accessibility to different tree species within a short distance, species replication varied from only one to three individuals. Tables 11.1 and 11.3 provide the information on the number of trees monitored in each study.

Both studies were conducted at the Marchantaria Island, located in the Central Amazonia region, upstream from Manaus on the Solimões River, just before the confluence with the Rio Negro. The island is 23 m a.s.l. and has an average annual period of inundation of 200 days (Worbes 1992).

11.2 Seasonality of Xylem Flux in Evergreen Versus Deciduous Trees

Measurements using the constant heating method and Granier sensors for determination of total water fluxes (Granier 1985, 1987) of selected tree species from a várzea inundation forest, have indicated that xylem sap flux density (Js) was positively correlated with the above stand diurnal variation of vapor pressure deficit (VPD; Parolin et al. 2005). Increasing above stand, or upper canopy VPD lead to an increase in Js and total sap flow, and vice versa. This relationship varied during flooding (Horna 2002 and unpublished data). In all evergreen trees, during phases of full crown expansion total sap flow of the terrestrial period did not exceed sap flow of the aquatic period.

Data of continuous water uptake in different várzea species over a complete year were used for a comparison of the seasonal behavior of evergreen and deciduous species (Horna 2002). It was hypothesized that if flooding induces water stress, reduced water uptake and stomatal closure of várzea trees during flooding is to be expected. Stomata closure would induce different physiological responses in evergreen and in deciduous trees with respect to tree water uptake. Evergreen species were expected to show a gradual reduction of tree transpiration versus vapor pressure gradient during flooding. At the end of flooding reversed effects were expected. For deciduous species reduced transpiration rates with stomatal control were expected with the onset of flooding and before leaves were shed.

As predicted, the seasonal course of Js was strongly influenced by tree phenology in the deciduous species studied. The annual cycle of Js is presented in Fig. 11.1 for four deciduous tree species and for one evergreen species. After leaf flush Js rapidly increased in all deciduous trees. High Js rates were observed throughout the beginning of flooding in March when deciduous trees still have most of their foliage. The deciduous tree species *Albizia multiflora* reached its maximum daily Js of 140 g H_2O $m^{-2}{}_{sapwood}s^{-1}$ in August after renewing all foliage and still under high flooding. Xylem sap flux and thus transpiration of deciduous trees was high and not significantly reduced by the onset of forest floor flooding as long as the main foliage was present. When leaf fall set in, tree transpiration in *Pseudobombax munguba*, *Albizia multiflora* and *Crataeva benthamii* was only slowly reduced, reflecting the rather gradual loss of foliage. During the late phase of leaf shedding, only *Pseudobombax munguba* and *Crataeva benthamii* showed an almost complete shutdown in tree transpiration with Js values of 5–10 g H_2O $m^{-2}{}_{sapwood}s^{-1}$. In contrast to deciduous species, evergreens did not show a reduction of sap flux during flooding which contradicted the paradigm of flooding stress. Parolin (1997) showed that at some periods during flooding the rates photosynthetic assimilation could be as high as the rates recorded during the dry period in várzea evergreen tree species. Leaf shedding and new leaf production are simultaneous processes in evergreen species occurring during flooding.

Vapor pressure deficit was well correlated with Js for species with different phenology patterns in the studied várzea forest (Fig. 11.2). The evergreen *Nectandra amazonum* showed a linear increase in Js with VPD up to1.5 kPa and no signs of stomata control were revealed. In the mesophytic *Pseudobombax munguba*, an efficient reduction of tree transpiration during conditions of ample soil water supply was observed above a VPD of 1.5 kPa, indicating efficient stomatal control to avoid excessive water loss. Besides, evidence of stomatal control in *Pseudobombax munguba* was already observed at the beginning of flooding (before leaf area reduction) when sap flux rates were slightly reduced in spite of the still maintained full foliage (Fig. 11.2). For *Pseudobombax munguba*, the relationship of Js to VPD was described by a non-linear regression of the form $Y = Y_0X/(b + X)$ which showed not xylem flux limitation by VPD.

11.3 Sap Flux and Stem Water Storage

Parolin et al. (2005) studied the patterns of stem water storage and refilling in six different várzea species. The calculation of the total amount of water stored in tree stems was based on the difference between parallel measurements of Js using Granier type sensors installed at the base of the stem and in the crown, on different main branches. On sunny days, during the non-flooded period, daily courses of basal and branch sap flow exhibited similar overall trends among all trees. Sap flow

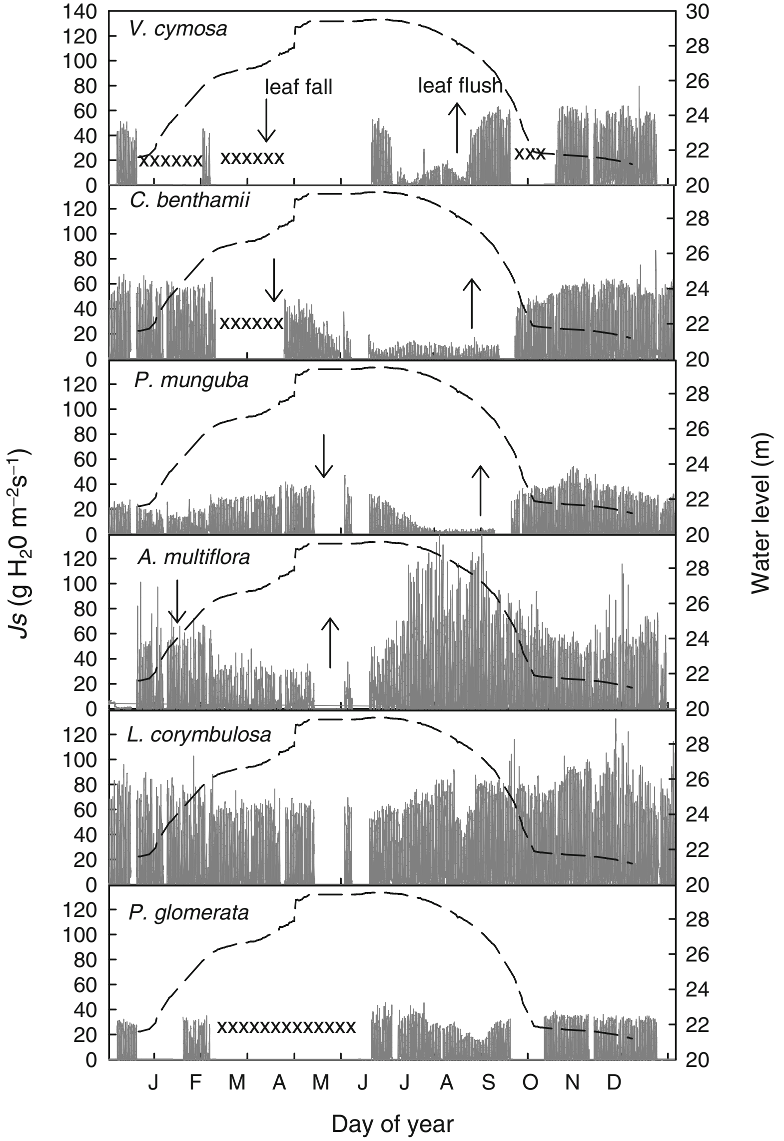

Fig. 11.1 Annual variation in water level at the Camaleão Lake and Js rates of four deciduous and one evergreen tree species studied at the várzea forest of the Marchantaria Island. The arrows indicate dates when leaf fall and leaf flush set on for deciduous trees. For the evergreen *Laetia corymbulosa* and *Pouteria glomerata* leaf exchange was continuous. Bars with crosses are periods of missing data due to malfunctioning of the equipment

raised rapidly in the morning with increasing photosynthetic photon flux density (PPFD) and VPD and decreased sharply in the early afternoon in all trees. However, the initial morning rise in basal sap flow lagged between ~0 and 1.0 h behind that

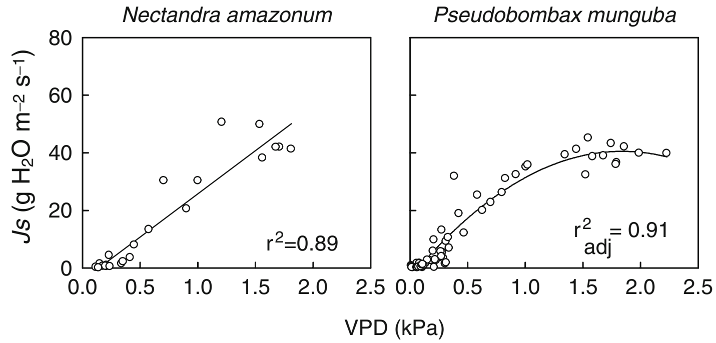

Fig. 11.2 Relationship between vapor pressure deficit and Js rates for the evergreen *Nectandra amazonum* and the deciduous *Pseudobombax munguba*. In *Nectandra amazonum* the relationship was explained by a linear regression, while in *Pseudobombax munguba* a non- linear regression of the form: $Y = Y_0X/(b + X)$, fitted the data better. These measurements were taken on a day within the period of increasing water level (February–April). At this time *Pseudobombax munguba* had still full foliage

of branch sap flow, depending on the individual. The time lag between attainment of maximum sap flow rates in the upper branches and at the base of the stem tended to be even larger, ranging from 1 to 2 h in deciduous trees such as *Tabebuia barbata*, *Crataeva benthamii* and *Pseudobombax munguba*, while in the evergreen *Nectandra amazonum* lag time was about 0.5 h (Fig. 11.3).

In the afternoon, the decrease in sap flow tended to occur earlier in branches than at the base of the stem, consistent with the morning trend. The difference in the lag phase between branch sap flow and basal sap flow suggested the capacity to stored water in the stem varied that species in and with season. Two species with contrasting phenology pattern are presented for comparison in Fig. 11.3. In October flooding had already ended and soils had drained while between March and April, water level was augmenting. During most years trees already stand in water since the beginning of March. The deciduous *Pseudobombax munguba* started dropping leaves at beginning of April (Schöngart et al. 2002). In *Nectandra amazonum*, the diurnal pattern of Js and the lag period between branch sap flow and basal sap flow did not differ with seasonality of flooding. This species did not show recharge of water in the stem and since water was normally available in the soil, trees did not exhibit a need to develop water storage strategies. The observed occurrence of Js during night hours may correspond to events of high VPD. These periods were frequent in October during the dry season. In the deciduous *Pseudobombax munguba*, a pronounce difference in the lag period between basal sap flow and branch sap flow was displayed. During October, the lag time lasted only 0.5 h. In comparison, during April branch sap flow started 2 h earlier than basal sap flow. In the afternoon, during October, branch sap

→

Fig. 11.3 (continued) deciduous species *Pseudobombax munguba*. Shaded areas on the left side represent measured higher stem base sap flow than branch sap flow. In the afternoons this corresponds to water refilling in the stem. To the right side are the differences in xylem flow between branches and stem base. Non flooded conditions occurred in October and during March April soil was flooded. *Pseudobombax munguba* had still most of its foliage during April

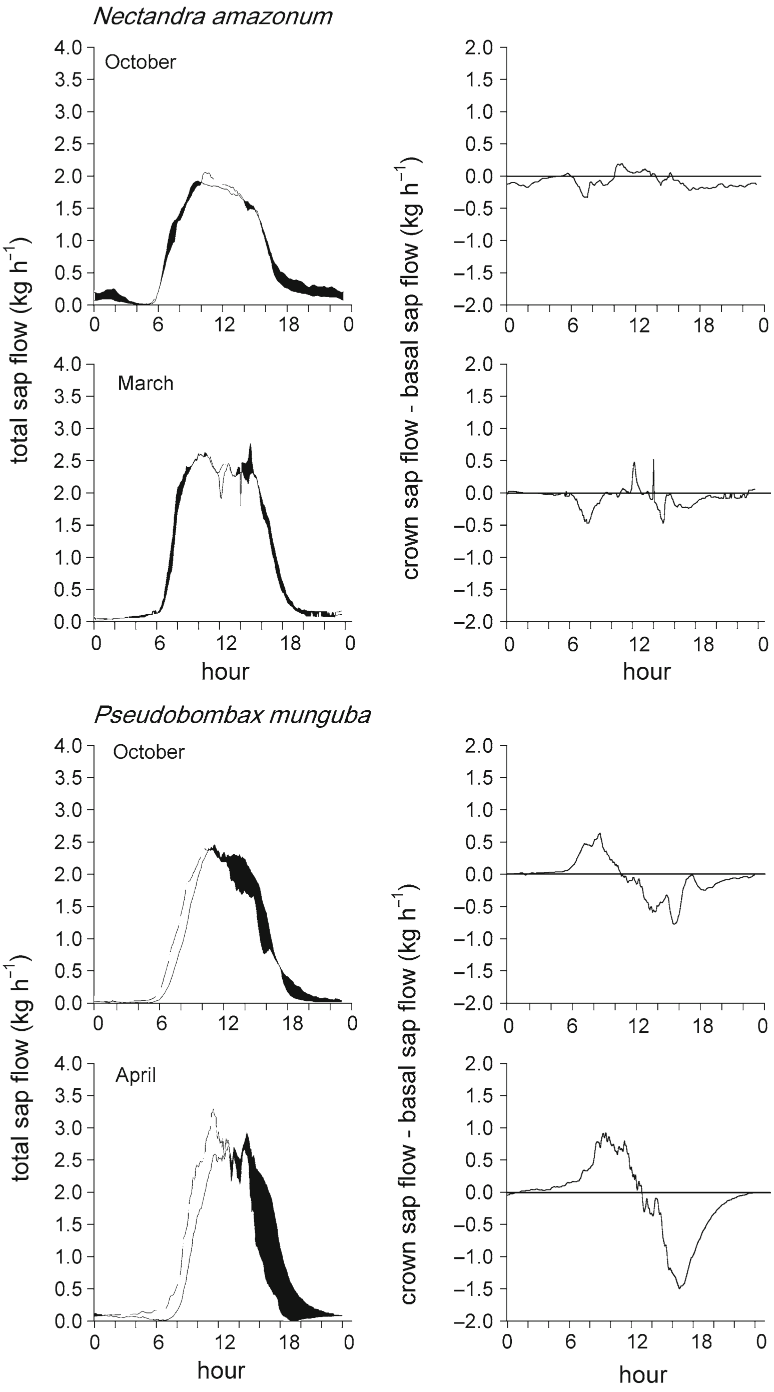

Fig. 11.3 Seasonal delay time of daily total sap flow between branches and stem base as an indicator for stem water usage for the evergreen species *Nectandra amazonum*, and for the

flow finished 2–3 h earlier than basal sap flow, while in April basal sap flow endured for 4–5 h after branch sap flow had stopped. This difference coincided with relative higher rates of Js during early flooding. It seemed that during the period of flooding and at the beginning of leaf fall *Pseudobombax munguba* built large water storage by extending the refilling time. On the other side, root activity obviously remained unaffected by flooding since water transport at the stem base continued into the night.

Basal sap flow in all trees typically returned to zero before 04:00 h, suggesting that nocturnal recharge of sapwood water storage was essentially completed. The total diurnal water storage capacity differed between trees, during the aquatic period ranging from 0 kg in *Nectandra amazonum* to 4.7 kg in *Pseudobombax munguba*. This represented up to 22% of the total daily water loss in the latter species. In other tropical trees, e.g. *Cecropia longipes* and *Anacardium excelsum*, storage was only 15% of total daily water loss (Goldstein et al. 1998). Night time was always sufficient for refilling the xylem water of the stems, with the exception of the evergreen *Laetia corymbulosa* where night time refilling was not completed after a series of days with high radiation and high VPD.

No significant influence of waterlogging on branch sap flow (which scales up to crown transpiration, Becker 1996) could be observed within 18 months of monitoring. The diurnal pattern of crown sap flow (a surrogate for transpiration) was influenced by the size of the internal water reservoir. Individuals having larger internal water storage capacity maintained maximum or near maximum transpiration rates for a longer period of time (*Pseudobombax munguba*). The dimension of the stem water stores was always sufficient to maintain crown transpiration and reservoirs had always been refilled during the night. Water limitation obviously did not lead directly to drought damage on leaves but may indirectly trigger leaf-shedding e.g. by hormone signals.

11.4 Sap Flux Area

Trees exhibited very different patterns of water transfer within the sapwood. These patterns are related to the distribution and size of the conducting units (Granier et al. 1996a). In temperate ring porous oak trees (*Quercus petraea*), 80% of the sap flow circulates in the outer 1 cm of stem cross sectional-area (Granier et al. 1996a). In the temperate diffuse porous *Fagus sylvatica*, however, the hydroactive area can go as deep as 22 cm in large trees (more than 50 cm DBH), but water transport decreases sharply towards the inner part of the stem (Hoelscher et al. 2005). Meinzer (2005) [AU1] analyzed the variability in the relationship between total cross-sectional area (basal area) and the area of wood that actually conducts water (sapwood area) over a range of plant functional groups across tropical and temperate species. They found that this relationship could vary within species depending on plant size and with different growth environments. For the 17 tropical species included in the analysis, sapwood area was about 72% of the stem basal area, with tree stems being as big as 1.3 m in diameter. In contrast, sapwood constituted only 43% of stem basal area in temperate conifers like *Abies grandis*, *Pinus ponderosa* and *Tsuga heterophylla*. In the temperate angiosperm *Quercus garryana* and in two other temperate conifers (*Pseudotsuga menziesii* and *Thuja plicata*) sapwood area was only 15% of stem basal area.

Table 11.1 List of the species analyzed (in alphabetical order) in the study of Parolin et al (2005), including data on tree phenology type (Schöngart et al. 2002), number of sampled individuals (n), tree diameter at 1.3 m height (DBH), stem sapwood area (SSA), percentage of sapwood area in relation to total stem basal area, correlation coefficient (r^2) of the relationship between SSA and stem radius, and percentage of trees that did not show an evident reaction to the coloring treatment. The regression between SSA and stem radius follows the form $Y = Y_o X^b$ according to Meinzer (2005)

			DBH (cm)		Sapwood thickness (mm)		SSA (cm²)				
Species	Phenology type	n	mean	sd	mean	sd	mean	sd	SSA (%)	SSA versuss radius (r²)	Indiv. with no reaction (%)
Laetia corymbulosa	Evergreen	22	15.1	4	16	6	76.1	29	42.5	0.54	22.7
Nectandra amazonum	Evergreen	18	19.6	9	29	36	94.9	49	31.5	0.90	11.1
Crataeva benthamii	Deciduous	16	13.7	4	17	3	72.9	28	49.5	0.92	0.0
Tabebuia barbata	Deciduous	14	15.9	6	16	6	81.9	51	41.3	0.86	0.0
Vitex cymosa	Deciduous	20	15.2	4	17	4	83.2	33	45.9	0.85	10.0
Albizia multiflora	Deciduous	18	20.1	7	30	52	109.0	56	34.4	0.81	16.7
Pseudobombax munguba	Deciduous stem-succulent	30	19.8	9	38	57	138.6	99	45.0	0.91	6.7

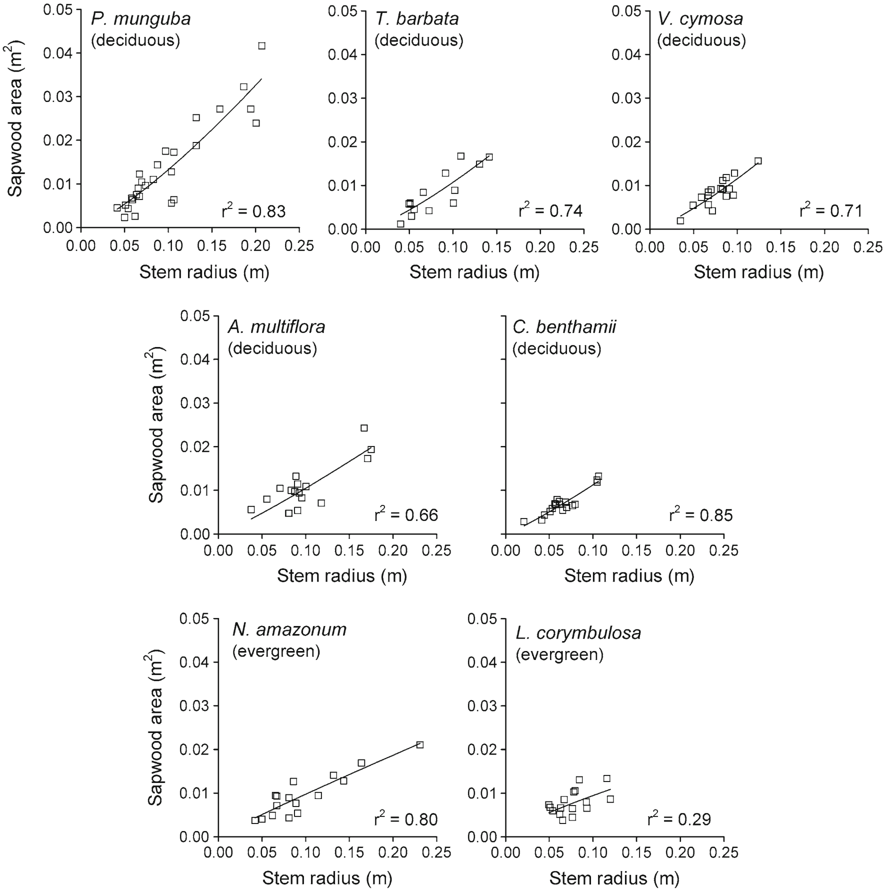

Fig. 11.4 Correlation between stem radius (m) and sapwood area for seven várzea tree species

In central Amazonian floodplain forests, sapwood thickness of seven common tree species measured by Parolin et al. (2008) ranged from 16 to 38 mm (Table 11.1). Sapwood depth at breast height was estimated using a staining method (Goldstein et al. 1998; Meinzer 2005). Colour was injected before midday to take advantage of the expected high transpiration rates and to allow for a good distribution of the applied dye. For all the species monitored by Parolin et al. (2008), a good relationship between sapwood area and stem radius was found (Fig. 11.4). Similar to Meinzer (2005), the dependence of sapwood area on stem radius was non-linear and described by a power function with an equation of the form $Y = Y_0X^b$, where Y is sapwood area, Y_0 is a normalization constant, X is stem radius, and b is the allometric scaling exponent.

Sapwood thickness did not vary much between individuals of one species. Mean active sapwood area ranged from 73 cm² in *Crataeva benthamii* to 139 cm² in *Pseudobombax munguba* (Table 11.1). These values are within the lower range of sapwood areas measured in trees of tropical uplands (Granier et al. 1996b; Andrade and Meinzer 1998; Goldstein et al. 1998; Anhuf et al. 1999; Rollenbeck and Anhuf

Table 11.2 Existing literature data on mean stem sapwood area (SSA) of different tree species of tropical, Mediterranean, and temperate forests

Study	Forest type/location	SSA (cm²)	DBH (cm)
Granier et al. 1996b	Tropical rain forest, French Guiana	103–796	13.4–58.2
Anhuf et al. 1999	Tropical forest, Venezuela	26–646	10.2–67.5
Goldstein et al. 1998	Tropical forest, Panama	200–5,100	19.7–101.8
Motzer et al. 2005	Tropical montane rainforest, Ecuador	21–1,352	6.1–45
This study	Tropical floodplain forest, Brazil	73–139	7–46.2
Meinzer et al. 1999	Brazilian cerrado, Brazil	6–39	5–10
Loustau et al. 1996	Mediterranean forest, Portugal	32–67	34.3[a]
Granier et al. 1994	Mediterranean forest, France	147–293	–
Granier et al. 1990	Mediterranean forest, France	181–533	–
Lu et al. 1995	Temperate forest, Norway	99–275	–

[a] Mean value

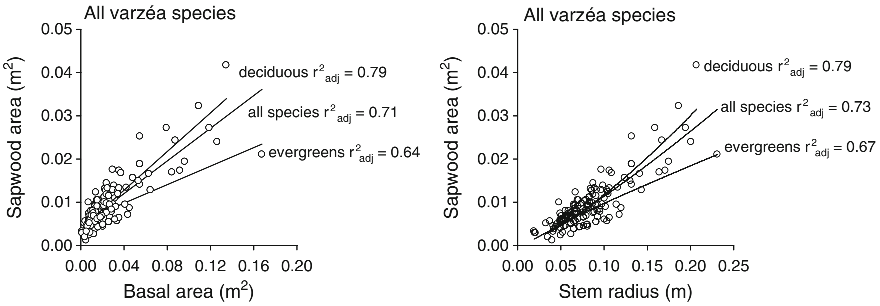

Fig. 11.5 Basal sapwood area in relation to (**a**) total stem basal area and (**b**) stem radius for deciduous, evergreen and all várzea species together. Line in (**a**) is the least-squares regression with a slope of: 0.19 for all trees, 0.22 for deciduous trees and 0.11 for evergreens. The regression in (**b**) follows the form $Y = Y_o X^b$ according to Meinzer (2005)

2007; Table 11.2), tropical montane (Motzer et al. 2005), temperate (Lu et al. 1995), or Mediterranean forests (Granier et al. 1990). They are larger than the sapwood area of trees of early successional tropical forests (Goldstein et al. 1998), Brazilian cerrado (Meinzer et al. 1999), or other group of Mediterranean forests studied by Loustau et al. (1996).

Correlations between sapwood area and stem radius were significant for all species and also for the two phenological groups. Correlation coefficients were very good in all species with the exception of *Laetia corymbulosa* (r^2 0.29) (Fig. 11.4). The coefficients of the power relationship of stem radius and sapwood area differed between evergreens ($Y_0 = 0.26$, $b = 1.36$) and deciduous ($Y_0 = 0.08$, $b = 0.92$) and were even lower than the values reported by Meinzer (2005) for ring porous *Quercus garryana* and the conifers *Pseudotsuga menziesii* and *Thuja plicata*. Similarly, the fraction of total basal area that was estimated as sapwood area was very low in comparison to the results presented by Meinzer (2005). The slope of this relationship, when grouping all várzea species was very low (0.18; Fig. 11.5).

When the species were grouped into deciduous (*Pseudobombax munguba, Albizia multiflora, Tabebuia barbata, Vitex cymosa,* and *Crataeva benthamii*) and evergreens (*Nectandra amazonum* and *Laetia corymbulosa*) the corresponding slopes values were 0.22 and 0.10 (Fig. 11.5).

The fact that only the stem-succulent (deciduous) tree, *Pseudobombax munguba* (Schöngart et al. 2002), had the largest active sapwood area and thickness (139 cm^2, Table 11.1) indicates that this species exhibits adaptive strategies different than other deciduous species (Parolin et al. 2008). In the case of *Pseudobombax munguba*, phenology and growth rhythm is triggered by precipitation (Schöngart et al. 2002) and not by the flood pulse or different external factors like in other deciduous species (Worbes 1999; Borchert and Rivera 2001).

11.5 Stand Transpiration

Stand transpiration of várzea forest, was estimated by Horna et al. (submitted) based on upscaling of xylem flux rates of individual tree species and on estimations of sapwood area. The latter based on the relationship between sapwood area and stem diameter for deciduous and evergreens. Stand sapwood area was estimated to be 8.6 m^2 ha^{-1} and a daily mean xylem flux rate 0.8 kg m^{-2} day^{-1}. Annual transpiration was estimated on 283.5 mm. This is a low value if compared with other references for Amazon rainforests (Rollenbeck and Anhuf 2007). However, in the case of várzea forest we have to take into account that trees are relatively small in comparison to other terra firme forest. Additionally, várzea forests have a large proportion of deciduous species losing their foliage during early flooding and growing new leaves during high flooding. For some trees this means up to 3 months without foliage (Schöngart et al. 2002) and consequently very low transpiration rates.

11.6 Stem Respiration

In várzea forest ecosystem, apical and stem diameter growth of trees generally follows the periodicity in forest soil flooding. Worbes (1992) reported dormancy in stem growth during maximum flooding and the beginning of cambial activity at the end of flooding. Some tree species, like *Crataeva benthamii*, *Tabebuia barbata*, *Vitex cymosa*, and *Pseudobombax munguba*, are more pronounced in their seasonality of growth, and show partial or complete leaf shedding during the flooding phase (Parolin 1997; Wittmann and Parolin 1999). Thus, it was suspected that the annual carbon gain must be small due to a low photosynthetic net uptake caused by flood induced leaf shedding or reduced photosynthetic performance (Waldhoff et al. 1998; Wittmann and Parolin 1999). However, there is no conclusive verification of a significant reduction in either stand leaf area or photosynthetic activity caused by flooding. Alternatively, the low carbon accumulation may be caused by a high respiratory carbon loss during periods of environmental stress or flooding. Further, due to the constant high ambient temperature regime in the study area with an annual average of 26°C, a high rate of respiratory carbon release might be assumed (Waring and Schlesinger 1985). In addition, the high contribution of living stem to total stand biomass may lead to the conclusion that the respiration rates of these components are in the same order of magnitude as total leaf respiration (Müller and Nielson 1965; Yoda 1967; Whitmore 1984; Sprugel and Benecke 1991). Estimates from Malhi and Grace (2000) for terra firme forest in the vicinity of Manaus suggest that 13.5% of the primary carbon production in these forest types is used for leaf respiration and 12.8% for wood respiration (stem and branches).

Horna (2001) studied the dependence of stem carbon release rates of the várzea trees with the ambient meteorological conditions, the phenological condition, and the seasonal flooding status of the site (Table 11.3). Site microclimate measurements included surface CO_2 exchange, and sap flux in the studied trees, as well as the forest light conditions and the flooding level. The gas exchange of woody tissue was measured with chambers connected to an open gas exchange system (ANARESY, Walz Co. 1998) with a LICOR 6262 infrared gas analyzer running in differential mode (Havranek 1981; Linder and Troeng 1981; Benecke 1985; Ryan et al. 1995). The seasonal variation in the relationship between carbon release and wood tissue temperature (Q_{10}) was observed during four distinctly water status situations of the year: (i) increasing water level "up", from February to April (89 days); (ii) "high" water level from May to July (92 days); (iii) decreasing water level "down", from August to October (92 days); (iv) "dry" forest floor, from November to January (92 days).

11.7 Stem Carbon Release in Relation to Phenology and Climate Variation

Stem carbon release rates showed a clear diurnal pattern during flooding that was more evident at the lower part of the stem. From the species studied, only the deciduous *Tabebuia barbata* showed a twofold increase in carbon release rates during the period of maximum flooding. Maximum carbon release rates occurred in the lower part of the stem of the evergreen *Nectandra amazonum* and in the deciduous *Albizia multiflora* during the onset of flooding (14 and 10 µmol CO_2 m^{-2} s^{-1} respectively). These were as well the largest individuals monitored. *Crataeva benthamii* and *Vitex cymosa* had the smallest variation in daily carbon release values for the entire study period with mean values ranging between 2 and 3 µmol CO_2 m^{-2} s^{-1}. The evergreen *Nectandra amazonum*, showed highest stem carbon release rates during high flooding in both, the lower (8 µmol CO_2 m^{-2} s^{-1}) and in the upper stem (10 µmol CO_2 m^{-2} s^{-1}). Other evergreen species like *Laetia corymbulosa* and *Pouteria glomerata*, and the deciduous trees *Pseudobombax munguba* and *Albizia multiflora*, had maximum stem carbon release during the beginning of flooding.

Table 11.3 Biometric measurements (DBH, diameter at 1.3m; H, tree height; SSA; stem sapwood area; V, stem volume, SWD, stem wood density; I, stem diameter increment) and growth respiration rates (R_g) calculated from I and ratio of corresponding fraction of CO_2 release due to growth from total stem respiration for different evergreen and deciduous tree species from the várzea forest at the Marchantaria Island, Manaus, Brazil (Horna 2002)

Tree species	DBH (cm)	H (m)	SSA (m^2)	V (m^3)	SWD ($g\ cm^{-3}$)	I (mm)	R_g ($\mu mol\ m^{-2}\ s^{-1}$)	Stem CO_2 (%)
Deciduous								
V. cymosa	15.4	14.6	5.9	0.29	0.45	2.64	0.40	5.6
C. benthamii	24.8	15.9	7.6	0.43	0.43	1.40	0.20	6.3
P. munguba	26.6	18.3	10.0	0.52	0.25	2.30	0.19	4.9
P. munguba	32.5	18.6	13.1	0.85	0.25	10.05	0.85	23.1
P. munguba	33.1	17.4	12.4	0.80	0.25	11.67	1.01	32.2
T. barbata	31.0	15.7	8.1	0.58	0.71	4.50	1.08	3.4
A. multiflora	52.9	17.1	12.1	1.46	0.65	7.10	1.56	7.3
Evergreen								
L. corymbulosa	13.4	14.2	3.3	0.08	0.54	1.00	0.18	4.0
L. corymbulosa	11.7	15.1	4.5	0.14	0.54	2.70	0.49	7.6
L. corymbulosa	15.7	15.5	4.6	0.14	0.61	2.55	0.52	9.9
P. glomerata	18.9	11.8	4.1	0.17	0.62	4.60	0.97	16.7
P. glomerata	18.1	12.3	9.8	0.31	0.66	2.65	0.59	11.5
N. amazonum	37.1	13.6	6.6	0.58	0.47	0.60	0.09	0.4

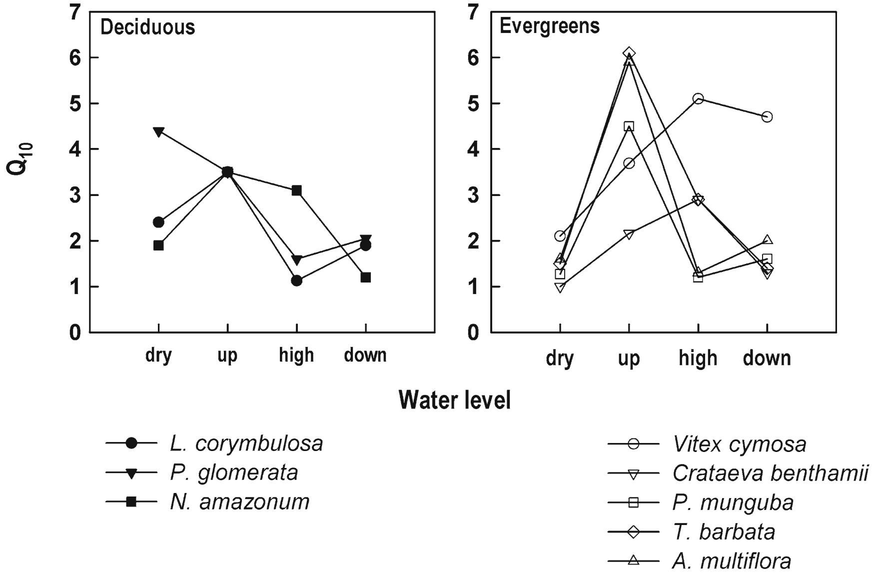

Fig. 11.6 Seasonal variation in Q_{10} values estimated for the stem of different evergreen and deciduous várzea trees. Seasons are related to the variation in flooding conditions at the study site. Q_{10} values were calculated from the response curves of CO_2 release rates to temperature variation over a period of 2–3 days per season

The response to temperature was variable among seasons. Species were more sensitive during the period of rising water level (Fig. 11.6). During high flooding the relationship between stem carbon release and stem temperature decreased and it was lowest during the dry season. The peculiar diurnal pattern of CO_2 release during the onset of flooding may be explained by an additional upward vertical transport of carbon dioxide in stems during flooding. Extremely high values were obtained, in some cases, for the correlation between stem woody tissue carbon release and temperature changes. Two species with contrasting phenology pattern are pictured in Fig. 11.7 during early and late flooding. A diurnal peak in stem CO_2 release was observed with the onset of flooding for both species. This effect was especially pronounced in the lower part of the stem. These high CO_2 release rates could not be explained only by temperature since woody tissue temperature did not vary much diurnally and seasonally and any known range of Q_{10} was not sufficient to explain this high CO_2 release. Two possibilities of an additional source of CO_2 can be considered: the first option was that additional carbon comes during flooding from a loss of carbon in structural biomass. This was not detected. The second option was that carbon is passively or actively transported from the roots to the lower stem sections and subsequently released into the atmosphere. A known path for the transport of gases is via intercellular gas space or aerenchyma tissue (Armstrong 1978). This path is known for several wetland species for the transport

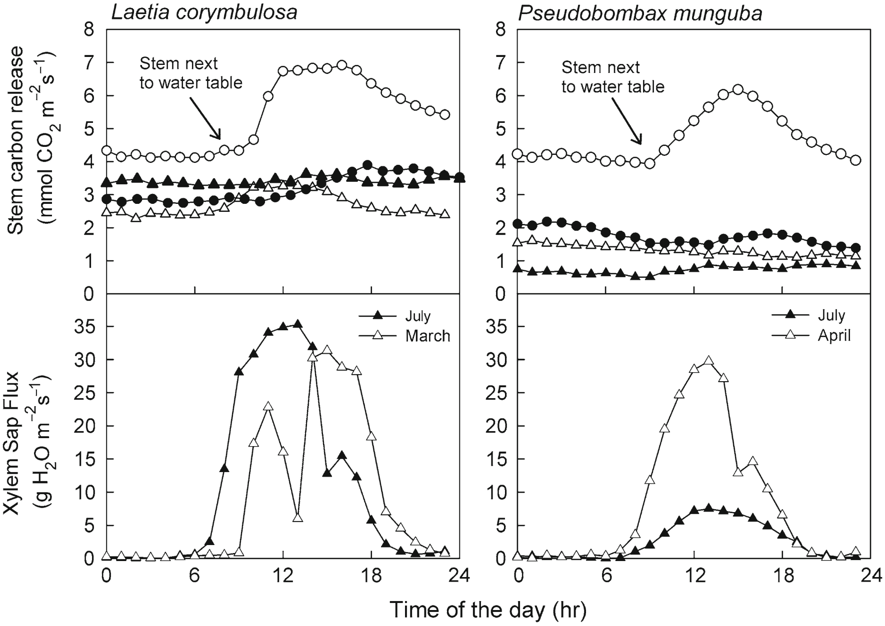

Fig. 11.7 Variation in CO_2 release with the onset of flooding at two locations in the stems of evergreen *Laetia corymbulosa* and deciduous *Pseudobombax munguba*. Daily xylem flux rates for the corresponding days of CO_2 release data. Open symbols are used for the period of high flooding (July) and full symbols are used for the early flooding phase (March–April). Circles are used for measurements located in the lower part of the stem and triangles for the upper stem (at approximately 8 m height, above the expected level of inundation)

between roots and shoots of oxygen, nitrogen and various metabolically generated gases such as carbon dioxide and ethylene. The risk of hypoxia because of deficient supply of oxygen under soil flooding or more complete plant submergence is reduced. It promotes radial oxygen loss from roots leading to oxidative detoxification of the rhizosphere. A second option was transport of CO_2 via xylem flux. The general possibility of a transport of dissolved CO_2 by xylem flow in trees had been noticed before (Negisi 1979; Meir 1996; Levy et al. 1999), but no correlations were described between seasonal effects and additional carbon release. In the last years a new path for the gas exchange between shoots and roots in flooded woody plants has been observed. The study of Stevens et al. (2002) showed that gas exchange was possible through the aerenchymatous phellem (cork) in flooded *Lythrum salicaria* L. This path provides an alternative path for the transport of gases after secondary growth when cortical aerenchyma usually perishes and is shred. This may be the case for some of the flooded trees in the várzea forest of the Amazon, however no references are available about the presence and development of aerenchymatous phellem for the species studied.

11.8 Respiration Components

We estimated the growth component of respiration (Rg) from the measurement of growth rates using the increment in stem diameter and assuming 50% carbon content in ash-free dry weight (Edwards et al. 1980; Ryan et al. 1994) and 25% of carbon needed to produce new tissue (Penning de Vries 1975). Maintenance respiration (Rm) was the difference between total respiration and growth respiration. The recorded growth rates were applied to a 7-month period (September - March) of observed stem growth as determined by Schöngart et al. (2002). Growth respiration was calculated from the calculated amount of new tissue produced per year (Table 11.3). Contrary to the expected low growth respiration during flooding, that coincides with the dormancy period of stem diameter increment (Worbes 1983; Parolin 1997; Schöngart et al. 2002), a high CO_2 release was measured at all lower stem positions at the beginning of flooding. The contribution of stem growth respiration to total stem CO_2 release was highest in the two *Pseudobombax munguba* trees (23–32%). For all other trees the contribution of stem growth respiration was below 15%. Total growth respiration was less than 30% of total carbon release for all studied trees. Values of growth respiration for temperate broadleaf species vary between 40% and 60% from total respiration (Edwards and Hanson 1996).

In spite of the fact that almost no stem increment growth occurs in the várzea forests during high flooding, the periods of dormancy are not clear from looking at the stem CO_2 release rates. Worbes (1997) predicted high respiration rates in várzea forest based on the observed contrast between low wood production and the high net primary productivity (NPP) of trees. With the measurements of stem CO_2 release, it became clear that growth respiration of stems was very low. This observation may indicate high maintenance respiration costs for várzea trees. During flooding, plants have to compensate the anaerobic conditions by anatomic and metabolic adaptations since the switch from aerobic to anaerobic respiration leads to a limited energy supply, a higher demand for stored carbohydrates, and the production of toxic substances (Worbes 1986; Schlüter 1989; Nilsen and Orcutt 1996). From these observations, it could be argued that várzea species similar to temperate broadleaf species (Edwards and Hanson 1996) are well adapted to flooding at the expense of high respiration rates and cambial dormancy.

11.9 Discussion and Conclusions

Xylem flux in várzea species followed the seasonality in leaf phenology. Continuous long-term decrease of water fluxes could only be observed in deciduous species with increasing leaf shedding during the aquatic period. However, no causal correlation between limited water supply to transpiring leaves and the observed leaf shedding could be verified. Leaf shedding did not follow decreasing xylem water fluxes but sap fluxes lessened simultaneously with continuous leaf shedding.

The occurrence of stem water storage was more notorious in deciduous species than in evergreen species. Stem water was filled up during night time and during extended periods at the beginning of flooding. Since water shortage was not the case under flooding, and the continuity of xylem flux indicated an active functioning of the root system for water uptake, no clear explanation is available for the presence of a water storage mechanism. However we suspect that this may be related to the initiation of new foliage development during high flooding. Another factor not taken into account in our study of várzea trees is the capacity to store water in the stem parenchyma. As Scholz et al. (2007) showed for Cerrado species, stem parenchyma is also involved in stem water storage, but at much lower degree than sapwood tissue. More important, based on the more negative osmotic potentials measured in the outer parenchyma than in the sapwood, Scholz et al. (2007) suggested that the parenchyma may serve as a storage reservoir for soluble carbohydrates. This type of storage may be expected in species like *Pseudobombax munguba* were parenchyma could be as deep as 2 cm in large trees (personal observation) and would help explaining the capacity of deciduous trees to growth new leaves during high flooding. Additionally differences in storage capacity in várzea trees would be related to stem wood density. According to Scholz et al. (2007) a 50% change in wood density was accompanied by a 400% change in sapwood capacitance or water storage capacity.

Reported values of sapwood area for tropical trees are very variable. Sapwood area may cover almost 100% of the cross sectional area in some tropical forest species (Goldstein et al. 1998; Phillips et al. 2001). In Amazonian terra firme trees, Dünisch and Morais (2002) found 36% for *Swietenia macrophylla*, 78% in *Cedrela odorata* and 93% in *Carapa guianensis* of the basal area to be hydroactive. For eight species in the Venezuelan rain forest, Rollenbeck and Anhuf (2007) reported a maximum ratio of 40% between stem sapwood area and cross sectional area. In the case of várzea trees sapwood area was less than 50% of the stem basal area (Parolin et al. 2008). Since stem increment in várzea trees is restricted to the terrestrial phase (Worbes 1997; Schöngart et al. 2002) it may be suspected that water transport occurs mainly in the new vessels. These are produced during each dry phase which is a typical behavior of ring porous xylem type. However, the development of new leaves during the aquatic phase and before the beginning of cambial activity (Schöngart et al. 2002) is in disagreement with the concept of ring porous xylem. In ring porous xylem type, cambial activity precedes leaf development by 2–4 weeks (Carlquist 2001).

Regarding carbon release in várzea forest, it could be concluded that high CO_2 release during all flooding stages (up, high and down) may be due to a combination of two cumulative factors: (i) High carbon dioxide release from branches during new leaf development. This release occurs in most várzea species during high flood or at the end of flooding; (ii) Additional efflux of CO_2 during early flooding which is attributed to vertical transport of dissolved CO_2 with ascending xylem sap. A relatively low CO_2 release occurred during the dry season (4 months to maximum 5 months) while during the different levels of flooding, the values were higher. It was confirmed that variation in CO_2 release is associated with variation in flooding.

Stem-CO_2 release did not respond to leaf phenology but lower stem release was clearly associated with flooding variation.

Várzea tree species are well adapted to the seasonal flooded conditions of the Amazon floodplain. Trees stand under water for several months every year and show no directly reduction in physiological activity unless associated with leaf fall in deciduous species. Xylem flux rates in evergreens area similar during flooding and dry periods. Deciduous trees recover their foliage during high flooding and immediately reach xylem flux rates as high as the ones observed during the dry season. However, stem CO_2 release rates are higher during flooding indicating a high respiratory demand and vertical transport of CO_2. This agrees with a functioning of trees under high metabolic demand due to stress under flooding. For deciduous species in addition, the development of new foliage before cambium activity, indicates that these species relay on carbon storage. Future research should focus on the seasonal pattern of carbon partitioning in várzea trees and an alternative anatomical path for CO_2 vertical transport and in relation to species phenology.

Chapter 12
Fruit and Seed Chemistry, Biomass and Dispersal

Pia Parolin, Danielle Waldhoff, and Maria T.F. Piedade

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Absract Fruits and seeds are released into the water and may be submerged or floating for several days to months – a situation which normally makes most seeds unviable. Trees are adapted and seeds remain visually sound for >2 months when continuously submerged. This stands in contrast to the majority of land plants, whose seeds quickly lose viability if submerged for prolonged periods. On the contrary, seeds of floodplain species kept in air dry or decompose within few days or weeks. Many species have high nutrient contents as a function of the relation to fish

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dispersal, just as in upland forests diaspores of species dispersed by mammals are rich in fat and proteins. However, in Amazonian floodplain trees dispersal syndromes are closely linked to water, with all necessary adaptations enhancing floatation and attractiveness for fish. High nutrient contents are also advantageous for the seedling, because a high investment of the parent tree into seed reserves guarantees fast initial growth. This can be crucial in an environment with a flood amplitude exceeding 10m. Time for seedling establishment in the non flooded terrestrial period is reduced to few months or weeks. For a fast and well timed establishment, seeds must germinate fast and they need adequate nutrient reserves.

12.1 Introduction

Fruit and seed characteristics are of extreme importance for the diet of fish and for germination and establishment strategies, and thus for the resulting patterns of forest regeneration in Amazonian floodplains. With a flooded period of up to 7 months, fruits and/or seeds are almost always released into the water and have to cope with being submerged or floating for several days to months – a situation which normally makes most seeds unviable (Hook 1984). The trees are adapted to this. In several species (*Aldina latifolia, Campsiandra comosa, Cecropia latiloba, Crataeva benthamii, Mora paraensis, Nectandra amazonum, Senna reticulata, Swartzia polyphylla, Vatairea guianensis, Vitex cymosa*) seeds remained visually sound at least for more than 2 months when continuously submerged (Parolin and Junk 2002). Other species, e.g. *Crudia amazonica* and *Tabebuia barbata*, had viable seeds at least for 1 month, but most seeds started to rot thereafter. This stands in contrast to the majority of land plants, whose seeds quickly lose viability if submerged for prolonged periods (Hook 1984). On the contrary, seeds of floodplain species which were kept in air, dry or decompose within a few days (e.g. *Tabebuia barbata*, *Nectandra amazonum*) or weeks (e.g. *Senna reticulata, Aldina latifolia;* Parolin, pers. obs.).

Under such extreme conditions, seed dispersal has to be efficient, which in Amazonian floodplains is often directed towards using the available dispersal vectors: water and fish. In fact, hydro- and ichthyochory are the main means of dispersal (Gottsberger 1978; Goulding 1980; Kubitzki and Ziburski 1994; Ziburski 1991). The diaspores show morphological adaptations which enhance floatation, like spongy tissues or large air-filled spaces (Kubitzki and Ziburski 1994; Williamson et al. 1999a,b; Williamson and Costa 2000).

Once a seed has been deposited, duration and timing of germination are the next steps for efficient establishment (Oliveira-Wittmann et al. 2010). With a flood amplitude exceeding 10 m, the time for seedling establishment in the non flooded terrestrial period is reduced to a few months or weeks. For a fast and well timed establishment, the seeds must germinate fast, which implies that adequate nutrient reserves in the seeds must be available, especially in nutrient poor environments like black water floodplains. In the present chapter, the role of fruit and seed chemistry and dispersal modes, and in the following chapter establishment (Oliveira-Wittmann et al. 2010) is analyzed.

12.2 Fruit and Seed Chemistry

The main components of fruits and/or seeds which are of interest because of their nutritional values are carbohydrates, protein, fat, and various cations such as potassium, sodium, calcium and magnesium.

Water mostly makes up the biggest part of the fruits: the individual fruit water content ranged from a maximum of 88% (*Vitex cymosa*) to a minimum of *Myrciaria* sp. with 1.9%. Fruits with high protein, fat and energy levels tend to have a water content which is far below the average, for example *Pseudobombax munguba* with a water content of 35%. A contrary situation exists among fruits with a high water content, which normally have high levels of carbohydrates and relatively little protein and fat, for example *Psidium acutangulum* with a water content of 73%. The fruits of the palm *Astrocaryum jauari* (Table 12.1) pulp and seeds consist to their major part of water and carbohydrates, with a high percentage of fat (14.7%) in the seed (Piedade 1985; Piedade et al. 2003, 2006).

Carbohydrates: The seeds of *Vitex cymosa*, *Crataeva benthamii* and *Pseudobombax munguba* have high sugar and starch contents (Table 12.2), an important energy resource for fast germination and seedling establishment.

Protein and fat: Fruits with a high nutritional value are those with relatively high levels of crude protein and crude fat. The nutritional value of the seeds of such fruits is considerably higher than the corresponding pericarp or testa. Fruits with an average nutritional value have a smaller discrepancy between the contents of pericarp and seeds. Balick (1985) examined oil-producing palms from the Amazon area

Table 12.1 Chemical analysis of fruits of *Astrocaryum jauari*. Results in g 100 g^{-1} of fresh weight (average). Analyses by Nutritional Department of INPA/Manaus, Brazil (From Piedade et al. 2006)

Fruit part	Water content (%)	Proteins (%)	Fat (%)	Ash (%)	Carbohydrates (%)	Calories (kcal)	Vitamin A (U.I 100 g^{-1})
Pulp (with peel)	60.0	3.2	3.2	2.2	31.4	167.2	8,500
Seed	42.4	3.2	14.7	0.8	61.1	389.5	not det

Table 12.2 Total soluble sugar and starch contents (average) of the seeds of seven common tree species of the Ilha de Marchantaria (From Koshikene 2005)

Species	Total soluble sugar (mg g^{-1})	Starch (mg g^{-1})
Vitex cymosa	28.53	15.02
Crataeva benthamii	26.65	12.88
Pseudobombax munguba	18.26	16.40
Guazuma ulmifolia	17.38	8.17
Cecropia latiloba	12.72	9.29
Salix martiana	3.58	4.28
Crescentia amazonica	0.50	1.81

(in *Astrocaryum jauari* he found an oil content of 36%). In fruits of *Cecropia latiloba* (Fig. 12.1) there are contradicting measurements of protein content: Saint-Paul and Soares (1995) measured 18%, in a range of 11% (*Vitex cymosa*) to 36% (*Pseudobombax munguba*). Waldhoff et al. (1996) measured a crude protein content of 22.5%, and Roubach (1995) says that the fruit of *Cecropia* sp. was the one that presented the lowest crude protein (4.1%) and lipid (0.9%) content in its composition, as well as a very high water content. The chemical composition of 19 analysed fruits of tree species from central Amazonian floodplains showed that seeds are, as expected, richer in crude protein and crude fat than the pericarp, which is itself richer in crude fibre (Table 12.3; Waldhoff et al. 1996 and Waldhoff and Furch 1999).

Fig. 12.1 *Cecropia latiloba* canopy with almost mature fruits

Table 12.3 Details of chemical composition and water contents (in percentage of dry mass) of seeds and fruits of 19 analysed tree species from Amazonian floodplains (Waldhoff et al. 1996; Waldhoff and Furch 1999; Parolin 2002d)

	Percentage of dry mass
Average soluble carbohydrates	67.3
Average crude fibre	29.6
Average crude protein	6.5
Average crude fat	18.9
Average crude ash	5
Average polyphenols	6.1
Average fruit water content	63
Average seed water content	47
Average energy	21.2 kJ g^{-1}

Table 12.4 Main cations of selected fruit species (From Waldhoff 1991)

Species	Analysed part	K^+	Mg^{2+}	Ca^{2+}	Na^+
Aldina latifolia	Fruit peel	319.4	67.4	66.2	0.7
	Seed	244.6	59.5	78.1	1.3
Annona montana	Fruit peel	742.5	93.9	90.1	1.2
	Seed	580.4	81.3	74.8	1.3
Astrocaryum jauari igapó	Fruit peel	524.0	41.5	33.4	1.4
	Seed	298.0	66.5	48.3	1.3
Astrocaryum jauari várzea	Fruit peel	966.5	96.1	109.7	4.3
	Seed	298.8	64.4	53.3	3.8
Casearia sp.	Fruit peel	1912.5	84.6	167.0	5.9
	Seed	274.0	66.8	36.0	1.5
Cecropia latiloba	Whole fruit	251.4	65.8	99.6	2.2
Crataeva benthamii	Fruit peel	763.5	58.4	56.4	3.5
	Seed	1379.0	85.7	62.0	3.3
Hevea spruceana	Seed	505.0	128.4	47.7	1.8
	Testa	190.1	10.5	24.4	1.6
Macrolobium acaciifolium	Fruit peel	527.6	39.2	395.5	2.1
	Seed	644.0	92.3	144.0	1.2
Ocotea cymbarum	Fruit peel	247.8	23.1	9.0	1.7
	Seed	485.4	40.4	17.3	2.0
	Testa	623.0	77.2	66.8	3.4
Pseudobombax munguba	Whole fruit	688.0	384.5	37.2	1.4
Psidium sp.	Fruit peel	905.5	52.1	93.1	32.6
	Seed	542.4	53.7	4.5	17.7
Symmeria paniculata	Whole fruit	526.0	86.8	157.0	2.3
Vitex cymosa	Whole fruit	561.5	53.4	35.9	1.4

Cations: Waldhoff (1991) analysed the main cations in 13 tree species (Table 12.4), and in all analysed fruits, the cation with the highest concentrations was potassium (K^+) and with the lowest concentrations was sodium (Na^+). Between species, differences are very big: potassium concentrations vary between 1,912.5 and 244.6 ppm, magnesium from 384.5 to 10.5 ppm, calcium from 395.5 to 9 ppm, and sodium from 32.8 to 1.2 ppm.

The high nutritional value of most species may be related to the ichthyochoric dispersal syndrome, as e.g. the fruits of the palm *Astrocaryum jauari* (Table 12.1). Especially the high contents of vitamin A may be advantageous for fish to put up stock reserves in form of fat which are needed for gonad development in the low water period when food resources are scarce. Goulding (1980) found 52 entire fruits of *A. jauari* in only one individual of the fish *Colossoma macropomum*.

The study by Waldhoff et al. (1996) with 30 species analysed cites the following main findings:

1. Fruits demonstrated in the majority of cases high protein and fat contents in the seeds, and high levels of soluble carbohydrates in the pericarp. Crude ash and crude fibre show no single tendency. Crude protein and crude fat are the critical nutrients in the chemical composition of a fruit, because they are the most important

energy sources. Carbohydrates deliver comparatively less energy; they are immediately metabolised and not stored (Rehm and Espig 1976).

2. The energy content is higher in the seeds than in the pericarp. Golley (1961) tested 600 plants and concluded that coniferous seeds had the highest energy level at 23.5–29.7 kJ g^{-1}. Of the plants of the inundated forest examined, *Hevea* sp. seeds have the highest energy content (32.3 kJ g^{-1}), followed by *Annona montana* seeds (25.6 kJ g^{-1}), *Astrocaryum jauari* (24.8 kJ g^{-1}) and *Pyrenoglyphus maraja* (24.4 kJ g^{-1}). These seeds are among those with the highest energy levels known. All these seeds are preferred by fish.
3. The water content of fruits and seeds rich in crude protein and crude fat is normally less than of fruits rich in soluble carbohydrates.
4. Nutritionally rich seeds (with a high level of protein and fat) normally have a nutritionally poor pericarp (high crude fibre level).
5. The phosphate content is higher in the seeds than in the pericarp. The average for measured phosphate concentration in fruits eaten by fish is 0.14% dry matter, which conforms to the ranges determined by Allen (1974) of 0.05–0.3%.
6. The polyphenol content is usually lower in the seeds than in the pericarp. This is to be expected considering the role of phenols (protection against animal consumption, Lodge 1991).
7. The crude ash content in fruits is generally low.
8. Seeds which are intact when excreted by fish are generally small; the corresponding pericarp has a higher nutrient level than the seeds, for example *Pouteria glomerata*.

12.3 Size and Biomass

Different variables (seed number per fruit, fruit and seed water contents, dry mass and sizes) were analysed in several species by different authors (Table 12.5). It becomes evident that the variables vary in part between studies, and they are extremely variable

Table 12.5 Mean (± standard error) fruit and seed mass and size of common tree species of the Ilha da Marchantaria, with more than three trees of each species and 20–50 fruits and/or seeds analysed, in alphabetical order by species. Level in flooding gradient: LV = low várzea with middle flooding of 6.7 m or 228 days per year, HV = high várzea with middle flooding of 2.4 m or 43 days per year (Data sources Waldhoff unpublished; Ziburski 1990; Waldhoff 1991; Waldhoff et al. 1996; Maia 1997; Waldhoff and Furch 1999; Parolin 2000b; Maia 2001; Nebel et al. 2001a,b; Ferreira 2002; Parolin 2002d; Wittmann 2002; Parolin et al. 2003; Koshikene 2005; Conserva 2006; Wittmann et al. in press

Fruit part	Water content (%)	Proteins (%)	Fat (%)	Ash (%)	Carbohydrates (%)	Calories (Kcal)	Vitamin A (U.I $100g^{-1}$)
Pulp (with peel)	60.0	3.2	3.2	2.2	31.4	167.2	8,500
Seed	42.4	3.2	14.7	0.8	61.1	389.5	not det

between species. Seed number for example varies from 1 per fruit (e.g. *Macrolobium acaciifolium*) to about 5,000 per infructescence (*Cecropia latiloba*).

Seed dry mass in Amazonian floodplain trees ranges over four orders of magnitude.

Mean dry seed masses ranged from 0.002 to 6.66 g in 31 species from 20 families typical for várzea, and in 27 species from 14 families from igapó it ranged from 0.008 to 69.36 g (Parolin 2000b). Conserva 2007 showed that Amazonian floodplain trees have a close relationship between seed mass/seed size and successional stage, early stages having typically (many) small seeds, whereas higher successional stages invest more in (few) large seeds with high nutrient reserves for the seedlings.

Seeds of different sizes are suited to different dispersal modes, germination strategies (Haig 1996) and establishment conditions (e.g. Salisbury 1942). Small seeds are advantageous because there are less limits to the amount of seed production, and the higher number of seeds allows to occupy more available microsites. Seedlings of large seeds are less subjected to physical disturbance by animals, damage by falling branches, litter or sediment layers, drought, darkness, and soil instability (Grubb and Coomes 1997). Large seeds allow higher rates of seedling establishment since they have more endosperm and are richer in energy reserves for the developing embryo (Moegenburg 1996). Small-seeded species are more abundant in the seed rain than large-seeded species, but only a weak negative relationship was found between seed size and survival from seedling emergence to adulthood (Moles and Westoby 2006).

12.4 Fruit Production and Its Timing

Data about fruit production are quite scarce. An overview on the annual fruit production of selected trees of várzea and igapó is given in Table 12.6 which shows that there is a large variety in fruit production between species, but there surely also is a large variety within species, and within years. No data are available concerning this.

The peak of fruit production occurs in the inundation phase, at high water. In *Pouteria glomerata* and *Ilex inundata*, berry dispersal starts with the onset of the high water season, while the berries of *Psidium acutangulum* fruit in the middle, and the drupes of *Vitex cymosa* towards the end of inundation (Waldhoff et al. 1996). Fruit dispersal (with 4–9 berries m^{-2}) of *Pouteria glomerata* lasts over 2 months, with a peak after 2 weeks. This corresponds to a maximum mass of 447 g m^{-2}. Fruiting of *Ilex inundata* lasts over 13 weeks, starting slowly with an increase after 7 weeks. Maximum dispersal rate is 765 berries m^{-2}, corresponding to 157 g m^{-2}. Diaspores of *Psidium acutangulum* are released in the middle of June with a high number of 42 berries m^{-2}, corresponding to 475 g m^{-2}. There is almost a linear decrease in fruit dispersal which stops after 4 weeks. In *Vitex cymosa,* during a 5-week trial, there was only a small variation in the dispersal rate between 113 and 159 drupes m^{-2}, corresponding to 205–323 g m^{-2}.

Table 12.6 Annual average fruit production of trees from várzea and igapó (From Maia 2001)

Species	Fruit production (kg ha^{-1})
Annona hypoglauca	1,930
Astrocaryum jauari	1,650
Bactris maraja	70
Cassia leiandra	1,850
Cecropia latiloba	1,280
Crataeva benthamii	2,362
Crescentia amazonica	15
Euterpe oleracea	1,158
Euterpe oleracea (cultivated)	15,000
Eschweilera tenuifolia	426
Grias peruviana	2,300
Hevea spruceana	55
Ilex riparia	673
Macrolobium acaciifolium	950
Macrolobium multijugum	120
Laetia corymbulosa	420
Myrciaria dubia	9,500–12,600
Mauritia flexuosa	6,000–20,000
Pouteria glomerata	1,512
Pseudobombax munguba	2,200
Psidium acutangulum	1,026
Spondias lutea	600
Vitex cymosa	227–1,223

12.5 Ecological Implications of Seed Mass and Size

In a comparative study (Parolin 2000b), seed masses of 31 species from várzea and 27 species from igapó were compared considering also their taxonomic relatedness. Overall average seed mass was higher (mean = 7.08 g) in nutrient-poor igapó than in nutrient-rich várzea (mean = 1.16 g). In igapó, the species growing at high elevations on the flooding gradient had significantly higher seed masses than the species growing at low elevations. In várzea, no difference was found between species growing at high and low elevations. Four large-seeded species from igapó occurring at high elevations on the flooding gradient were responsible for most of the difference in average seed mass between forest types. These data suggest that at low positions in the flooding gradient in igapó, selection pressure on seed size is probably the same as in várzea. At sites with short periods of flooding in igapó forests, on high levels in the flooding gradient, the need for rapid height growth may have selected for species with larger seeds which enable seedlings to be less dependent on soil nutrients. The size of diaspores may also play a role for dispersal: seeds of buoyant species with smaller seeds require less water for dispersal than large seeded species (Moegenburg 2002).

12.6 Dispersal

Fruit and seed types cover all possible forms, ranging from pods (e.g. *Albizia multiflora*) over capsules (e.g. *Alchornea* spp.), drupes (e.g. *Andira inermis*), berries (e.g. *Aniba affinis*, *Annona* spp., *Astrocaryum jauari*) to pyxidia (e.g. *Eschweilera* spp.) (Table 12.5). Fruit dry mass ranges from 0.01 g (*Salix martiana*) to 96g (*Mora paraensis*), seed dry mass ranges from 0.008 g (*Mollia speciosa*) to 69 g (*Aldina latifolia*). All means of dispersal common to trees are represented in Amazonian floodplains. However, most tree species of Amazonian floodplains display adaptations (e.g. air-containing tissue or hairs or very light seeds) to take advantage of the seasonal flood pulse for dispersal. Thus, hydro- and ichthyochory are the main means of dispersal (Gottsberger 1978; Goulding 1980; Ziburski 1991; Kubitzki and Ziburski 1994).

12.6.1 Hydrochory

There is obviously a dominant trend towards water dispersal of diaspores with buoyant tissues (Fig. 12.2). There is evidence of this in the design of many fruits, and many others that seem aimed at other vectors may still nevertheless be capable of water dispersion. Colourful and fleshy fruits – obvious signals for animal dispersion – may also be light and buoyant and can float along in streams. And in fact, some studies have shown that some fruit that would be assumed to be animal dispersed are indeed often dispersed by water (Ziburski 1991). Tests on the different floating capabilities were performed by Ziburski (1991), and by Waldhoff et al. (1996) using scanning electron microscopy on fresh material. The results show that e.g. *Annona montana* seeds have a single row of air-containing tissues, *Hevea spruceana*

Fig. 12.2 Fruits, seeds (**a**) and spongy tissue (**b**) of the fruit of *Aldina latifolia*, which enhances flotation (Photo Pia Parolin, May 1994)

Fig. 12.3 Floating fruits near meadows or mats consisting of macrophytes, plant fragments, woody debris etc. (Photo Pia Parolin, Janauari May 1994)

seeds have a series of rows with air-containing tissues, *Macrolobium acaciifolium* has a series of air-containing tissues in the fruit casing and *Cecropia latiloba* has many hairs which retain air and so enable them to float.

Submerged objects reduced the distance dispersed but not the probability of dispersal (Moegenburg 2002). In the palm genus *Leopoldinia*, in contrast to most other palms, the mature fruits of riverine species are lighter than water and do not loose their buoyancy after the decay of the fleshy portion of the fruit – a clear adaptation to dispersal by water (Kubitzki 1991).

The long period of floatation without loss of viability which is characteristic for most species may result also in the formation of “floating seed banks” (Marques 1994; Fig. 12.3). In várzea, soil seed banks are not formed by any species with the exception of *Cecropia* spp. (Ziburski 1991) and do not play the important role they have in temperate ecosystems, where the role of propagule banks (seeds on or in soil) in maintaining biodiversity in floodplains is very relevant (Leck 1989; Middleton 2000). It must be emphasised that the problem with aquatic dispersal is that it operates almost exclusively in a downstream direction. Upstream dispersal requires other agents, such as fish, turtles, other reptiles, or wind (Kubitzki 1985a).

12.6.2 Ichthyochory

The dispersal by fish has an importance comparable to the classic dispersal of seeds by birds and mammals in upland forests. Fish use the resources in the aquatic–terrestrial transition zone. When the floodplain forests inundate, frugivorous fishes congregate beneath trees and consume fruits that fall into the water.

Table 12.7 Fishes feeding on *Astrocaryum jauari* fruits in Amazonian black-water floodplains of the Anavilhanas Archipelago at high water (May–July) (Data from Goulding 1980, 1983 from stomach content fish analyses performed at the Anavilhanas Ecological Station, from interviews with local people, and from G. Borges and M.C.L.B. Ribeiro personal communication). xxx – high, xx – mean, x – low frequency (From Piedade et al. 2006)

			Exploitation of *Astrocaryum jauari*		
Fish species	Common name	Family	swallow	break	nag
Colossoma macropomum	Tambaqui	Characidae	xx	xxx	
Colossoma bidens	Pirapitinga	Characidae	xx	xxx	
Brycon sp.	Jatuarana	Characidae	x		x
Brycon cf. melanopterus	Matrinchão	Characidae	xx		x
Myleus spp./*Metynnis* spp.	Pacú	Characidae			xx
Serrasalmus spp.	Piranha	Characidae			x
Leporinus spp.	Aracú	Anostomidae			x
Phractocephalus hemiliopterus	Pirarara	Pimelodidae	xx	x	
Paulicea lutkeni	Pacamú (Jaú)	Pimelodidae	xx		x
Rhamdia schomburgkii	Jandiá	Pimelodidae	x		
Lithodoras dorsalis	Bacú-pedra	Doradidae	x		x
Megalodoras irwini	Rebeca	Doradidae	xx		
Oxydoras niger	Cuiu-cuiu	Doradidae	x		
Semaprochilodus spp.	Jaraqui	Prochilodontidae			x

Chemical signs are released by fallen fruit to attract fish (Araujo-Lima et al. 1998). Also the noise of fruits falling into water attracts fish (Veríssimo 1895). Many of the over 2,000 species of freshwater fish are dispersers of many rain forest fruits and depend on flooded forests for food; the question remains to what extent the forest regeneration depends on seed dispersal by fruit-eating fishes. Many fishes destroy the seeds, the most notorious seed eaters belonging to the genera *Brycon* and *Colossoma*. They have evolved an extraordinarily strong dentition which enables them to masticate even the hardest diaspores (Kubitzki 1985b). Gottsberger (1978) found that of 33 plant species studied, 16 had seeds that were not regularly broken by fish and 17 had seeds that were. The former seeds belong mainly to very primitive groups whereas the latter belonged mainly to more recent plant groups.

In *Astrocaryum jauari*, the fruits are eaten by at least 16 species of fish which either gnaw the pulp, fragment the seed, or ingest the entire fruit thus acting as dispersal agents (Table 12.7; Piedade et al. 2003, 2006). Ziburski (1990) analysed the role of two important fish species for dispersal, *Colossoma macropomum* and *Lithodoras dorsalis*. Table 12.8 shows the species and amount of fruits and seeds swallowed by these two fish species and the percentage of undestroyed diaspores after gut passage.

The primary role of fishes may be to remove fruit-pulp from seeds and to carry seeds against the prevailing water current (Anderson et al. 2005). Movements of *Brycon guatemalensis* were considered by Horn (1997) in Costa Rica a strategy to maintain *Ficus glabrata* distribution upstream.

Table 12.8 Species and amount of average tree fruits and seeds swallowed by *Colossoma macropomum* (n = 48 individuals) and *Lithodoras dorsalis* (n = 7 individuals), and percentage of undestroyed diaspores found in stomach and guts (Data from Ziburski 1990, Ilha de Marchantaria, in order by species)

	Colossoma macropomum		*Lithodoras dorsalis*	
Species	Weight of fruits/seeds (g)	Undestroyed seeds (%)	Weight of fruits/seeds (g)	Undestroyed seeds (%)
Annona hypoglauca			478.1	100
Annona sp.			695.7	100
Astrocaryum jauari			595.7	100
Cecropia latiloba	273.2	100	1,889.0	100
Crataeva benthamii	2198.7	49	554.3	100
Crescentia amazonica	423.8	97		
Duroia sp.			43.0	100
Macrolobium acaciifolium	31.9	0		
Nectandra amazonum	7.3	18		
Neolabatia cuprea	612.5	49	4.6	100
Pouteria sp.			40.0	100
Psidium acutangulum	592.9	99	1,297.2	100
Simaba orinocensis	1.1	100		
Vitex cymosa	54.2	97	0.6	100

Gut passage plays a major role for the breaking of dormancy, possibly by enzyme action, but only in few species (Ziburski 1991): some species have a significantly higher germination percentage (e.g., *Psychotria* sp., Mannheimer et al. 2003) in seeds removed from the intestine of fishes then in those from stomachs, but in other species (e.g. *Cecropia* sp.) no such differences were found. Ziburski (1991) found that out of 40 tree species only three really depended on fish for propagation (*Crataeva benthamii*, *Astrocaryum jauari* and *Crescentia amazonica*) – the other fruits may be propagated only occasionally by fish.

Among diaspores dispersed by fish, there is little uniformity in shape, texture, colour and taste, and it may be assumed that seed-eating by fish is highly opportunistic (Kubitzki 1985b).

12.6.3 Mammaliochory (Including Chiropterochory)

Mammals play important roles in the dispersal of Amazonian upland trees, and definitely play a big role also for floodplain trees, although the complex role that mammals play in creating and modifying seedshadows in tropical forests cannot be easily quantified (Stoner et al. 2007b). The role of large fruit-eating primates as dispersal agents of large seeds has been stressed by Haugaasen and Peres 2005, Gottsberger and Silberbauer-Gottsberger 2006, Nuñez-Iturri and Howe 2007. Julliot (1996) found that primates select brightly coloured fruit, and reject dull ones.

Fig. 12.4 *Swartzia argentea* seeds hanging on a long aril which enhances chiropterochory

Many primates (Terborgh 1990; Lambert and Garber 1998) and bats (Fleming and Heithaus 1981) swallow seeds whole (Fig. 12.4). They extract pulp from the fruit without destroying the seeds. Although primates are generally thought to be principally seed dispersers, several species are seed predators. Brown capuchins *(Cebus apella)* overcome seed protection mechanisms with their manipulative skills and strong jaw, and have a significant predatory impact on several plant species (Peres 1991).

In addition to bats and primates, many large mammals swallow seeds whole and hence contribute to the seed shadows of particular plant species in tropical regions (Stoner et al. 2007b). Terrestrial ungulates like red brocket deer (*Mazama americana*) and collared peccary (*Tayassu tajacu*) retreat to floodplain islands of the Amazon basin and shift from a frugivorous to a woody browse diet (Bodmer 1990). Peccaries bite off seeds and are the main source of mortality to the buriti palm *(Mauritia flexuosa)* (Antonik 2005).

12.6.4 Ornithochory

Several fruits of floodplain trees are arillate or berry-like, with a brightly coloured exterior or aril – which correspond to the fruit type that (Amazonian) birds prefer

(Gorchov et al. 1995). Amazonia hosts a big number of birds, many of which are migratory species (Petermann 1997). Some endemic species are typical in the floodplains: amongst others, the genus *Xiphorhynchus* (Aves: Dendrocolaptidae) is associated with seasonally flooded forest types in Amazonia (Aleixo 2006).

Birds play an important role for long distance dispersal in Amazonia (Macedo and Prance 1978; Snow 1981; Gorchov et al. 1995; Hayes and Sewlal 2004), e.g. between the palm tree *Euterpe oleracea* and parrots (Moegenburg and Levey 2003). The effectiveness of birds in long-distance dispersal (against the water currents?) in Amazonian floodplains is not known. In fact, the lower Amazon River is known to act as a barrier to migration for forest birds (Hayes and Sewlal 2004).

12.6.5 Anemochory and Autochory

In Amazonian floodplains, three groups of plants characteristically show a preponderance of adaptations for dispersal by wind, especially the emergent trees. Examples include many species of the Malvaceae/Bombacaceae (seeds surrounded with hairs), Bignoniaceae (with broadly winged lightweight seeds), legumes (with one-seeded, alate pods) and Vochysiaceae (with small, winged seeds) (Kubitzki 1985a).

Wind dispersed seeds are common, e.g. in *Salix martiana*, *Ceiba pentandra* or *Pseudobombax munguba* (Fig. 12.5; Kubitzki 1985a; Ayres 1993; Gribel and Gibbs

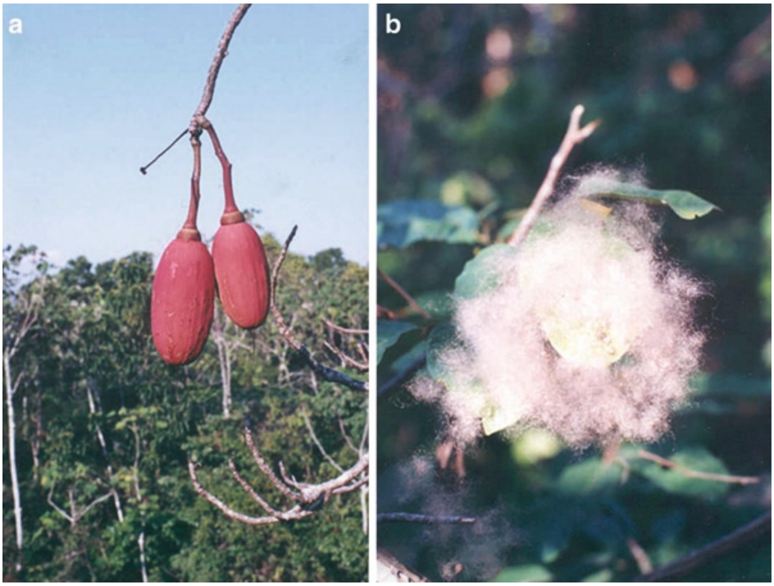

Fig. 12.5 Wind dispersed seeds of *Pseudobombax munguba*: (**a**) closed fruit, (**b**) seeds with hairs which enhance wind dispersal (Photo Pia Parolin, Ariaú August 1994)

2002; Oliveira and Piedade 2002) which produce a large quantity of small seeds provided with cotton-like hairs. Other anemochorous species typically are adapted for dispersal by wind by wings on the seed (*Couratari oligantha*), by alate drupes (*Triplaris surinamensis*), or minute seeds (*Calycophyllum spruceanum*) (Kubitzki 1985a; Mori and Brown 1994). The hairs and wings have been shown to increase the efficiency of wind dispersal (Andersen 1993) by decreasing fall velocity, either by increasing drag or by creating lift (Augspurger and Franson 1993). Often these seeds are dispersed in more than one way (Plitmann 1986). For example, *Pseudobombax munguba* (Malvaceae) has comose seeds which are carried away by the wind when the capsule opens (Pijl 1982). Many of its seeds, if not most, land in the water where some float away with the currents and others are eaten by fish (Ridley 1930). This species, however, would be classified as wind-, and not water-, dispersed because wind is the mechanism by which the seed departs from the mother plant (Mori and Brown 1994).

Autochory, the process of fruit and seed self-dispersal by means of physical expulsion, is quite common in Amazonian floodplains, although it has never been quantified and it is often difficult to separate this dispersal mode from other kinds, and from secondary dispersal.

In *Astrocaryum jauari* for example, the fruits fall off the palm tree and may be accumulated near the adult plant – a simple mechanism of barochory is prevalent here (Piedade et al. 2003). Other species like of the Euphorbiaceae family (*Hevea* spp., *Maprounea guianensis*) have active explosive mechanisms, where the ballistic fruits expulse their seeds to significant distances (Ducke 1949; Saravy et al. 2003). In *Hura crepitans*, maximum dispersal distance recorded was 45 m from the parent tree, with a marked modal dispersal distance at about 30 m (Swaine and Beer 1977).

12.7 Discussion

There is a large spectrum and variety of morphological, nutritional, and chemical traits of fruits and seeds among Amazonian floodplain trees. This diversity is not different from upland forests. Fruit and seed morphology varies greatly between species, and so does their nutritional value, which in many cases is very high as a function of the relation to fish dispersal, just as in upland forests mammal dispersed species are rich in fat and proteins. In contrast to upland forests, in Amazonian floodplain trees dispersal syndromes are closely linked to water, with all necessary adaptations enhancing floatation and attractiveness for fish. On the other hand, all typical dispersal syndromes of upland forests also occur in the floodplains. The relationship between morphological and chemical traits, and the relation of these traits to interactions with frugivores and to dispersal is understood for some species as was outlined in this chapter. Still, many details which can be relevant for establishment following dispersal are yet not understood. As just one example, the orientation and position of a diaspore on or in the soil surface influences germination (Peart 1981): seed orientation may confer an advantage during the seedling's establishment phase. To our knowledge, no one has ever considered this aspect in the establishment biology of any Amazonian floodplain tree species.

The role of all these traits and mechanisms for the occurrence of determined species in determined environments, e.g. along the flooding gradient in the "várzea alta" or "várzea baixa", or in the different existing ecosystems with many (várzea) or no (igapó) nutrients available in the soil, has been equally little analysed to date. Species distributions may be limited by substrate boundaries due to constraints at either the germination or seedling establishment life history stages (Wenk and Dawson 2007).

Despite the ongoing research, be it chemical analyses, or the study of dispersal biology or fruit morphology, no evidences exist of why exactly these species established in the floodplains instead of in the non-flooded adjacent uplands. We suppose that the fruits were not the focus of selection for floodplain areas, but more research could lead to different results.

Concluding, despite the enormous role of fruits and seeds for the regeneration of the forests, for the diets of animals and for the human population who hunts these animals or uses directly the fruits and seeds for their own diets, we still know very little and a lot of research has to be done.

Chapter 13
Seed Germination and Seedling Establishment of Amazonian Floodplain Trees

Astrid de Oliveira Wittmann, Aline Lopes, Auristela Dos Santos Conserva, Florian Wittmann, and Maria T.F. Piedade

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Abstract Many Amazonian floodplain trees fruit during the high-water period and thus benefit from long-distance dispersal by hydrographic corridors. Two different germination strategies can be observed: Species with buoyant seeds tend to germinate rapidly as soon as seeds get in contact with river waters, while species with submerged seeds generally undergo longer dormancies and germinate when flood-waters recede. In Amazonian floodplains, tree seedlings get frequently fully submerged for various periods, inducing hypoxia, complete darkness, and elevated

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mechanical constraints brought up by water currents and sediment. However, observations from field inventories indicate that seedlings of several várzea tree species perform very well under submergence, whereas mortality rates increase during the terrestrial phases. Establishment strategies seems to change along the flooding gradient: Seedlings from highly flooded low-várzea tree species are well-adapted to tolerate the seasonal inundations, while seedlings from low and irregularly flooded high-várzea tree species are poorly-flood adapted thus reacting very sensitive to flood pulse variations.

13.1 Introduction

In Amazonian floodplain forests, diaspores and seedlings get in contact with river water during varying periods, either by buoyancy or by submersion. While dispersal in many floodplain trees is linked to river waters and aquatic dispersers, establishment of trees is restricted to the terrestrial phases, which, depending on the location along the flooding gradient, may last only few months. In contrast to upland forests, where tree regeneration is mainly linked to the seedlings' demand for light (i.e., Budowski 1965; Bazzaz and Pickett 1980; Whitmore 1990; Bazzaz 1991), the recurrent inundation cycle in floodplains is considered the most restraining factor to seedling establishment (Junk et al. 1989; Klinge et al. 1990; Puhakka and Kalliola 1993). Young individuals remain frequently more than 6 months completely submerged (Oliveira Wittmann et al. 2007a). Thus, structure and composition of seedling and sapling communities in Amazonian floodplains are strongly related to height and duration of the annual floods (Wittmann and Junk 2003).

Studies tracing the initial phases of species development such as the seedling and sapling stage are scarce in Amazonian floodplains. However, taking only adult individuals as basis to explain species distribution and population structure dynamics can lead to mistakes, because many processes may occur very early in the life of a plant (Li et al. 1996; Zagt and Werger 1998). Studies on the regeneration of neotropical tree species are needed in a wide range of habitats because species composition and individual densities vary considerably in response to differences of environmental conditions at small scales, and are also regulated by mechanisms of seed predation and competition between species (Denslow 1980; Bruenig 1983; Bongers et al. 1988). In floodplain forest, tree regeneration occurs under closed canopies, in gaps, or in open areas like beaches on river shores, interfluvial channels, and lakes (Junk and Piedade 1997). While regeneration and growth of Amazonian upland trees are processes relatively well known, lasting from few years in pioneer species to up to several decades in late-succession species (Swaine and Whitmore 1988), there is little knowledge about growth of tree regeneration in Amazonian floodplain species.

Because of methodological restrictions, most studies on seedling establishment in floodplain forests are limited to relatively short observation periods in the terrestrial phases. However, several controlled experiments simulating flood conditions on seeds and seedlings have been performed, and the monitoring of seedling growth and development was accompanied in both, greenhouses and the field. This chapter summarizes the existing knowledge about the processes of seed germination and seedling establishment of Amazonian floodplain tree species, and provides new data from ongoing studies.

13.2 Germination in Buoyant and Submerged Seeds

Most Amazonian floodplain trees synchronize the peaks of fruit production with the seasonal changes of the river level, shedding fruits at high waters (Goulding 1983; Ayres 1993; Kubitzki and Ziburski 1994; Mannheimer et al. 2003; Parolin et al. 2010c). After dropping into the water, the diaspores are subjected to varying periods of buoyancy and/or submergence, with seeds floating during periods of up to 2 months (Kubitzki 1985a). Seed buoyancy and/or submergence increase the distance of dispersal by the river current, enhancing the probability of seed predation by fish and other aquatic dispersers (Goulding 1983). Diaspores are dispersed by water (hydrochory), sometimes associated to transport by air (anemochory), or by fishes (ichthyochory) (Gottsberger 1978; Pires and Prance 1985; Ziburski 1991; Kubitzki and Ziburski 1994; Piedade et al. 2006; Maia et al. 2007; Lucas 2008, Parolin et al. 2010b). The contact with the river water is interpreted to be the most important factor breaking seed dormancy in Amazonian floodplain tree species (Ziburski 1991; Scarano 1998). Non-floating seeds, however, submerge in a hypoxic or even anoxic environment, which deprives them of oxygen supply that is necessary to initiate germination (Frankland et al. 1987; Kozlowski and Pallardy 1997). In these species, dormancy in general is broken when seeds emerge at the beginning of the terrestrial phase.

Water absorption by imbibition cause re-hydration of seed tissues and intensification of respiration and other metabolic activities that produce the energy and nutrient budget necessary to the growth of the embryonic axis (Bryant 1985; Nassif et al. 1998). Water softens the tegument, which favors penetration of oxygen and allows the transfer of soluble nutrients to different parts of the seed (Toledo and Marcos Filho 1977; Fosket 1994). Under a physiologic point of view, germination is a transition from a state of rest to a situation of metabolic activity (Nassif et al. 1998), and it is expected that contact with water is favorable to the germination process. When dropping into the water, buoyant seeds may remain partially in contact with air, as for example, in the Amazonian várzea species *Salix martiana* and *Pseudobombax munguba* (Barroso et al. 1999; Conserva 2007; Oliveira Wittmann et al. 2007a) (Figs. 13.1 and 13.2). Other species, such as *Vitex cymosa*, *Crataeva benthamii*, *Crescentia amazonica* and *Pouteria glomerata*, however, disperse the entire fruits (Parolin 2000b; Piedade et al. 2006; Oliveira Wittmann et al. 2007a; Conserva 2007). Depending on the hardness of the epicarp, seeds of the latter species may remain floating or submerged without direct contact to river waters for varying periods.

The capacity of seed buoyancy in many Amazonian floodplain tree species was described by several authors (i.e., Gottsberger 1978; Goulding 1983; Ziburski 1991;

Fig. 13.1 (**a**) Mature fruit of *Pseudobombax munguba*; (**b**) Open fruit dispersing seeds involved by fruit fibers (kapok); (**c**) Seed involved by kapok landed on aquatic macrophytes

Kubitzki and Ziburski 1994; Parolin 2000b; Scarano et al. 2003; Koshikene 2005; Oliveira Wittmann et al. 2007a). Seed buoyancy does not appear to be related to specific seed sizes and weights (Parolin 2000b; Koshikene 2005; Parolin et al. 2010b), being more likely a genotypic adaptation to seasonal or permanent flooded environments (Pires and Prance 1985; Lopez 2001; Kozlowski 2002). In fact, germination of waterlogged seeds in most Amazonian floodplain tree species is associated to seed buoyancy. Only few tree species with non-floating seeds are known to germinate while submerged, as observed by Castro (2004) and Conserva (2007) in *Campsiandra comosa*, *Calycophyllum spruceanum*, and *Hura crepitans*. Both studies, however, used water columns of only 10 cm depth in the experimental setting, thus allowing full light reaching the submerged seeds. In addition, oxygen

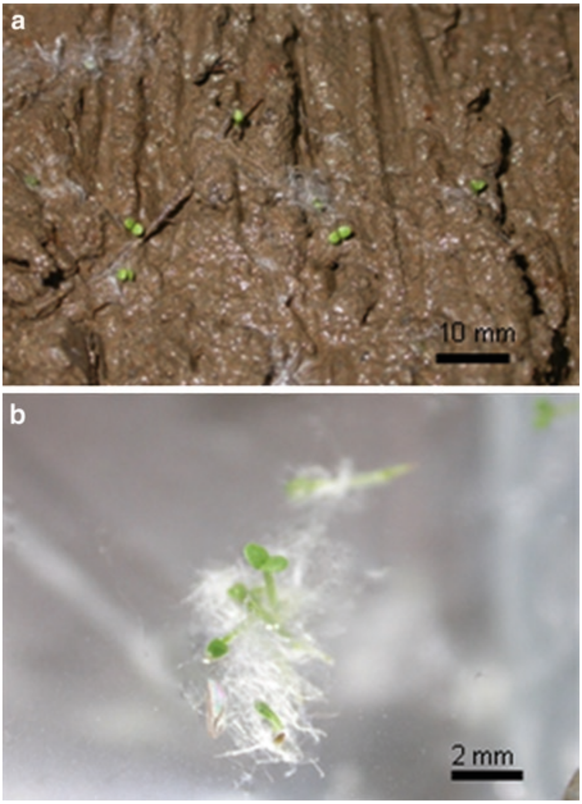

Fig. 13.2 Seedlings of *Salix martiana* germinated upon várzea substrate (**a**), and in water (**b**)

concentrations in the experiments might be higher than in the natural environment, where seeds undergo submersions by poorly transparent waters to depths of up to 10 m (Kubitzki and Ziburski 1994; Scarano 1998).

Besides oxygen availability through contact with air, and water, light is the most important factor influencing germination initiation in buoyant and submerged seeds. Light is generally considered a control sign over seed dormancy and germination (Bewley and Black 1982). In Amazonian floodplains, the start of germination determines the length of the growth period and fitness during the subsequent terrestrial phase (Pons 2000). Floating seeds may be exposed to direct sun light, and thus have the basic conditions to start germination while still in contact with river waters.

Some authors investigated germination in Amazonian floodplain trees according to the residence time of seeds in water (Lopez 2001; Scarano et al. 2003; Koshikene 2005; Conserva 2007; Oliveira-Wittmann et al. 2007a); others have used different substrates and methods in germination experiments (Kubitzki and Ziburski 1994; Scarano et al. 2003; Ferreira et al. 2005a). Since observation periods of waterlogging of the seeds ranged from 15 to 150 days (Table 13.1), comparisons of germination success are difficult. After 75 days, seeds of *Carapa guianensis* had germination

Table 13.1 Seed germination from experiments with Amazonian floodplain trees species upon distinct substrates, observed by different authors. IG = Occurrence in igapó forest, LV = Occurrence in low-várzea forest (mean inundation height >3 m, corresponding to an inundation period >50 days year^{-1}), HV = Occurrence in high-várzea forest (<3m, <50 days year^{-1})

Species	Habitat	No. of seeds per fruit (average)	Dry seed mass (mg)	Residence in water (days)	Start of germination (days)	Buoyancy	Germination while waterlogged	Germination rate (%)			Reference
								water	soil	other[a]	
Aldina latifolia Spruce ex Benth.	IG				18			0	55		Parolin (2001b)
Calycophylum spruceanum (Benth.) Hook f. ex K. Schum.	LV/HV	20		15	5	No	Yes		56		Conserva (2007)
								84			Conserva (2007)
Campsiandra comosa (Benth.)[c]	LV	9	6.129	15	60	Yes	Yes	55.5			Castro (2004)
											Parolin (2000b)
					24			0	20		Parolin (2001b)
Carapa guianensis Aubl.	HV			30	3	Yes	Yes	34		54	Scarano et al. (2003)
				60				58		24	Scarano et al. (2003)
				75				58		12	Scarano et al. (2003)
				10		Yes		>80			Lopes (2001)
				20				>70			Lopes (2001)
				60				<40			Lopes (2001)
Cecropia latiloba Miq.	LV	5436	0.50					91	82		Koshikene (2005)
					13			0	50		Parolin (2001b)
			0.002								Parolin (2000b)

Crataeva benthamii Eichler	LV	83	241					28	37		Koshikene (2005)
					8			0	40		Parolin (2001b)
						No				80	Kubitzki and Ziburski (1994)
			0.205								Parolin (2000b)
Crescentia amazonica Ducke	LV	359	5.82					5	4		Koshikene (2005)
						Yes				88	Kubitzki and Ziburski (1994)
			0.004								Parolin (2000b)
Crudia amazonica Spruce ex Benth.	IG/LV	1			18				0	40	Parolin (2001b)
Duroia duckei Huber	IG/LV	>100			19	No	No		53		Conserva (2007)
				15				37			Conserva (2007)
				45				1			Conserva (2007)
				90				2			Conserva (2007)
				120				2			Conserva (2007)

(continued)

Table 13.1 (continued)

Species	Habitat	No. of seeds per fruit (average)	Dry seed mass (mg)	Residence in water (days)	Start of germination (days)	Buoyancy	Germination while waterlogged	Germination rate (%)			Reference
								water	soil	other[a]	
Ficus anthelmintica Rich. ex DC.	LV	>100		60		No			11		Conserva (2007)
							No	3			Conserva (2007)
Guazuma ulmifolia Lam.	HV		4.28					13	9		Koshikene (2005)
Himathantus sucuuba (Spruce ex Müll. Arg.) Woodson	LV/HV	2									Koshikene (2005)
				15				98		94	Ferreira (2002)
H. sucuuba[b]				15				64		91	Ferreira et al. (2005a)
Hura crepitans L.	HV	15		60		Yes	No		13		Conserva (2007)
Ilex inundata Poepp. ex Reissek	LV	4			59	No	No		9		Conserva (2007)
				15				14			Conserva (2007)
				30				3			Conserva (2007)
				45				6			Conserva (2007)
				60				5			Conserva (2007)
				90				4			Conserva (2007)
			0.013								Parolin (2000b)

Laetia corymbulosa Spruce ex Benth.	LV	10		15	35	No	No	39	6		Oliveira-Wittmann et al. (2007a)
									21		Oliveira-Wittmann et al. (2007a)
				15		No	No	29			Conserva (2007)
				30				23			Conserva (2007)
				45				3			Conserva (2007)
				60				9			Conserva (2007)
				90				2			Conserva (2007)
						No				88	Kubitzki and Ziburski (1994)
			0.004								Parolin (2000b)
Macrolobium acaciifolium (Benth.) Benth.	IG/LV	1		15	3	Yes	Yes	100			Castro (2004)
			1.426								Parolin (2000b)
Mora paraensis Ducke	LV/HV				8			0	100		Parolin (2001b)

(continued)

Table 13.1 (continued)

Species	Habitat	No. of seeds per fruit (average)	Dry seed mass (mg)	Residence in water (days)	Start of germination (days)	Buoyancy	Germination while waterlogged	Germination rate (%)			Reference
								water	soil	other[a]	
Nectandra amazonum Nees	LV	1			15			0	55		Parolin (2001b)
Ocotea cymbarum Kunth	HV	1			23	No	No		27		Conserva (2007)
				30				11			Conserva (2007)
				60				24			Conserva (2007)
				90				21			Conserva (2007)
Pachira aquatica Aubl.	LV/HV	20		10		No		100			Lopes (2001)
				20				100			Lopes (2001)
				70				>80			Lopes (2001)
Piranhea trifoliata Baill.	LV	3			4	No	No		13		Conserva (2007)
				30				7			Conserva (2007)
				120				2			Conserva (2007)
				150				1			Conserva (2007)
			0.055								Parolin (2000b)
Pseudobombax munguba (Mart. & Zucc.) Dugand[d]	LV	634	22.4						92	97	Koshikene (2005)

P. munguba^{d}				15	5	Yes	Yes	90	42	Oliveira-Wittmann et al. (2007a)
P. munguba^{d}				15		Yes		61	41	Oliveira-Wittmann et al. (2007a)
									46	Conserva (2007)
P. munguba^{d}				15	3			8		Conserva (2007)
						Yes			100	Kubitzki and Ziburski (1994)
			0.013							Parolin (2000b)
Salix martiana Leyb.^{d}	LV	21	0.03					68	78	Koshikene (2005)
S. martiana^{d}				15	<1	Yes	Yes	96	80	Oliveira-Wittmann et al. (2007a)
S. martiana				15		Yes	Yes	98	51	Oliveira-Wittmann et al. (2007a)
			0.02							Parolin (2000b)

(continued)

Table 13.1 (continued)

Species	Habitat	No. of seeds per fruit (average)	Dry seed mass (mg)	Residence in water (days)	Start of germination (days)	Buoyancy	Germination while waterlogged	Germination rate (%)			Reference
								water	soil	other[a]	
Senna reticulata (Willd.) H.S. Irwin & Barneby	HV	25			5				0	85	Parolin (2001b)
Swartzia polyphylla DC.	IG/LV				8				0	90	Parolin (2001b)
Tabebuia barbata (E. Mey.) Sandwith	IG/LV	65			14	Yes	Yes			>90	Conserva (2007)
				30					>90		Conserva (2007)
				45					>90		Conserva (2007)
				60					47		Conserva (2007)
				90					30		Conserva (2007)
					10				0	50	Parolin (2001b)
Vatairea guianensis Aubl.	IG/LV/HV	1			5	Yes			0	100	Parolin (2001b)

Vitex cymosa Bert. ex Spreng.	LV	1							17	24	Koshikene (2005)
				15	18	No	No		52	33	Oliveira-Wittmann et al. (2007a)
						Yes					Kubitzki and Ziburski (1994)
											Parolin (2000b)
									0	60	Parolin (2001b)

[a] The other substrates utilized were: sand + sawdust in reference 3 and 4, moistened paper in reference 6, and vermiculite in reference 11

[b] Seeds derived from a tree growing in Amazonian terra firme

[c] Seeds without tegument

[d] Seeds without fruit fibers (kapok) that naturally involves them

rates of 58% (Scarano et al. 2003), whereas shorter periods of waterlogging resulted in lower germination rates. For the same species, Lopez (2001) reported germination rates of up to 80% after a period of waterlogging of only 10 days.

The wide range of seed viability and intra-specific germination variability indicates that more studies are required to better understand the influence of water on germination in floodplain tree species. After 90 days of seed buoyancy, germination rates in *Ocotea cymbarum* and *Tabebuia barbata* were 21% and 30%, respectively. For the same period, germination rates amounted to only 4% and 2% in buoyant seeds of *Ilex inundata* and *Laetia corymbulosa*, respectively (Conserva 2007). *Duroia duckei* presented viable seeds after 120 days of submersion and 1% of the seeds from *Piranhea trifoliata* germinated after 150 days of waterlogging. The seeds of these species are able to survive an entire aquatic phase to germinate in the following terrestrial phase. In contrast, other species show extremely short seed viability, such as *Salix martiana* with only 48 h after fruit opening. In this pioneer species, low seed viability is compensated by continuous fruit production during the year and by seedling emergence when seeds still float upon the water (Oliveira and Piedade 2002; Oliveira-Wittmann et al. 2007a, Fig. 13.2). In most of the performed germination experiments, waterlogging of seeds during varying periods resulted in faster germination and higher germination rates when compared to seeds placed in substrate (Parolin and Junk 2002; Scarano et al. 2003; Koshikene 2005; Oliveira Wittmann et al. 2007a). The only species which showed higher germination rates in the substrate than in water was *Crataeva benthamii* (Koshikene 2005), which has non-floating seeds. A synthesis of the results of studies on germination of 28 floodplain tree species is presented in Table 13.1.

In general, seed longevity in tropical rainforest trees is comparatively short, and most trees have non-dormant seeds (Ng 1978; Miquel 1987; Lopez 2001). However, dormancy of varying periods is common in many Amazonian floodplain trees. Independent if seeds are buoyant or submerge, the seeds of many Amazonian tree species remain viable after several months of waterlogging (Parolin and Junk 2002, Parolin et al. 2004b). This is in marked contrast to the majority of strictly terrestrial plants, whose seeds quickly loose viability if submerged for prolonged periods (Hook 1984; Parolin 2009). On the other hand, seeds of several Amazonian floodplain species dry and decompose within a few days (e.g., *Nectandra amazonum*, *Tabebuia barbata*), or weeks (e.g., *Senna reticulata*, *Aldina latifolia*) when kept in air (Parolin et al. 2006; Parolin 2009). In species that reproduce during the aquatic phase, regardless if the seeds float or sink, germination starts after the flood recedes (Ziburski 1991; Parolin et al. 2004b).

In summary, two different germination strategies can be observed in Amazonian floodplain trees: Species with buoyant seeds generally tend to germinate rapidly as soon seeds get in contact with river waters, which may enables seedlings to establish as soon they land on non-flooded substrates. Species with submerged seeds generally undergo longer dormancies, and germinate when flood-waters recede. Both strategies benefit from long-distance dispersal by hydrographic corridors. Many floodplain species, however, also occur in non-flooded environments, thus dispersal, germination, and establishment are not necessarily linked to flood waters.

Most germination experiments were performed in hydrochoric tree species that occur on highly flooded sites (e.g., low várzea). More comparative studies on germination of widely distributed species are needed in order to fully understand the impact of flood waters on specific germination.

13.3 Seedling Establishment

13.3.1 Establishment and Flooding

Tree species establishment in Amazonian floodplain forest was investigated in several studies, most of them investigating seedling survival, growth, and physiology under experimental waterlogging and submergence (i.e., Fernandes-Correa and Furch 1992; Schlüter et al. 1993; Waldhoff and Furch 1998; Waldhoff et al. 1998; Krack 2000; Maia et al. 2005; Parolin 2001a,b, 2002d; Ferreira 2002; Parolin and Junk 2002; Ferreira et al. 2005a; Koshikene 2005; Parolin et al. 2006; Oliveira Wittmann 2007; Oliveira Wittmann et al. 2007a; Conserva 2007; Maurenza 2007). In addition, some studies performed seedling and sapling inventories in Amazonian floodplain forest, all of them taking place in the várzea (Worbes 1986; Schlüter 1989; Nebel et al. 2001c, Wittmann and Junk 2003, Oliveira Wittmann et al. 2007b; Conserva 2007; Assis 2008; Marinho 2008).

Establishment occurs in buoyant seeds, when they land on substrate, or when submerged seeds emerge. While buoyant seeds of some species only produce radicles, and are not capable to establish (Kubitzki 1985a; Ferreira 2002; Parolin and Junk 2002; Scarano et al. 2003), *Hevea brasiliensis*, *Salix martiana* and *Pseudobombax munguba* form fully developed seedlings, emitting radicles, cotyledons, and primary leaves from buoyant seeds (Ziburski 1990; Oliveira 1998; Oliveira Wittmann et al. 2007a). This behavior may enhance fast seedling establishment, because plants are growing while the water is still receding (Oliveira Wittmann et al. 2007a; Parolin 2009). However, seedlings developed in water are often morphologically different from those that developed in substrate, because they lack photo-geotropism and produce strongly warped stalks (Oliveira Wittmann et al. 2007a, Fig. 13.3). Ziburski (1990) found that seedlings of *Hevea brasiliensis* and *Pseudobombax munguba*, formed while floating, rotted within a few days, or that viable seedlings could not protrude roots into the substrate when landed. However, it cannot be excluded that seedlings emerging from floating seeds may successfully establish when they get trapped by floating debris and associated organic material (Parolin 2009).

Contrasting to the situation in adult trees, which may maintain parts of photosynthetic organs in contact with the atmosphere, tree seedlings frequently get completely submerged for various periods, which may last up to 300 days year^{-1} (Schlüter et al. 1993). Complete submergence induces hypoxia or even anoxia, often associated to complete darkness and elevated mechanical constraints brought up by water currents and sediment. In addition, seedlings may undergo varying

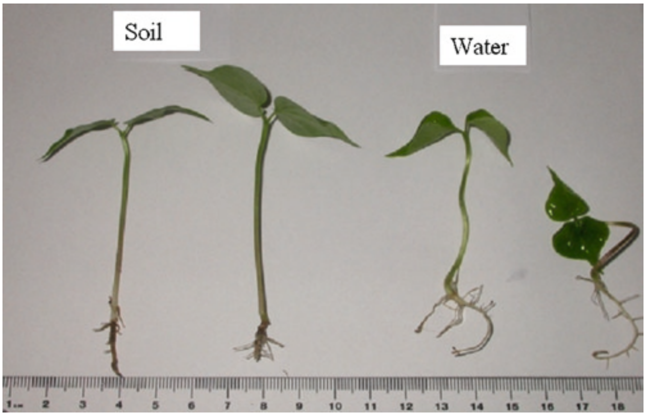

Fig. 13.3 Seedlings from *Pseudobombax munguba* developed from seeds in várzea substrate and in water (Oliveira Wittmann et al. 2007a)

periods of severe droughts when the low water periods coincide with the dry season. The multiple strategies and adaptations of Amazonian floodplain tree seedlings to complete submergence were recently summarized by Parolin (2009). Seedling performance during drought events is discussed in Parolin et al. (2010).

The few available observations in the natural environment together with experimental studies as summarized by Parolin (2009) indicate that seedlings not only tolerate, but perform very well under submergence. Oliveira Wittmann et al. (2004 unpublished) monitored establishment and height growth of seedlings of *Vitex cymosa* and *Eschweilera ovalifolia* in a low-várzea forest on Marchantaria Island, central Brazilian Amazon during two consecutive terrestrial phases, for a period of 390 days. In an area totaling 16 m^2, 459 individuals ≥10 cm height were inventoried. During 60 days of observation, height increases in *E. ovalifolia* averaged 10 cm, whereas *V. cymosa* seedlings did not significantly increase in height even after 390 days of observation (Fig. 13.4). After the aquatic phase, with an inundation height of up to 6 m and duration of 210 days, even a decrease in average seedling height was observed; this was due to mechanic disturbance that broke the apex in several individuals. Mortality rates after the aquatic phase averaged 11.1% in *E. ovalifolia*, but increased to 33% after the subsequent terrestrial phase. Mortality, however, was compensated by a new cohort of seedlings, maintaining the initial observed seedling density nearly constant. In *V. cymosa*, mortality rate after the aquatic phase was 2.5%, reaching 9.4% during the subsequent terrestrial phase. A new cohort of establishment increased seedling density from 18 to 24 individuals m^{-2} at the end of the observation period (Fig. 13.4).

By investigating establishment and growth behavior of 31 floodplain tree species during a period of 11 weeks, Parolin (2002d) proposed two distinct strategies of seedling establishment relating growth rates to the position of plants along the flood gradient. The first strategy refers to species which grow at highly inundated areas. They are tolerant to extended submersion and present slow growth

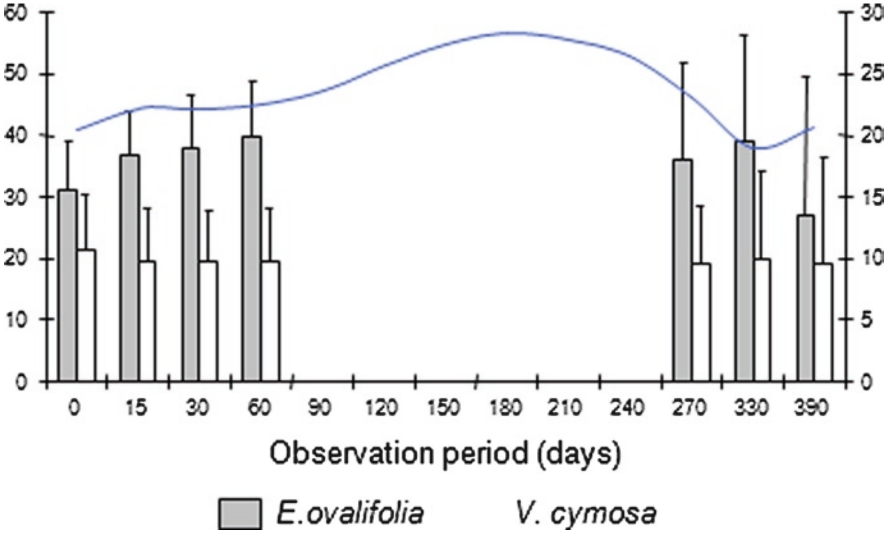

Fig. 13.4 Average height growth of seedlings of *Eschweilera ovalifolia* and *Vitex cymosa* during two consecutive terrestrial phases (±SD). The period from 60–270 days represents the aquatic phase

(low várzea species); the other strategy refers to species which grow on less flooded areas. These try to escape from submersion by fast growth to keep at least a part of the crown out of the water (high várzea species). However, after 11 weeks of observation only two species reached heights of more than 30 cm, both being characterized by wide distribution along the flood gradient. Oliveira Wittmann (2007) studied the growth of 19 várzea tree species, of which only *Apeiba glabra* and *Erythrina fusca* were restricted to the high várzea: Both species showed fast growth, reaching heights above 100 cm in 180 days of observation, corroborating Parolin's (2002d) postulation. Considering that in high várzea forest mean flood duration lasts for maximally 50–70 days per year (Wittmann et al. 2002b), these species would have a growth period longer than 290 days to escape from waterlogging or submersion.

13.3.2 Establishment and Habitat Dynamics

Due to the different disturbance regimes imposed by varying sediment loads of white-, black-, and clear-waters, and the associated distinct water chemistry of várzea and igapó (Junk and Piedade 2010), tree establishment substantially differs between both ecosystems. Seedlings may develop at sites where flood-levels exceed 10 m after flood waters recede (*Eugenia* sp., obs. F. Wittmann). However, the flood-induced tree lines are associated to different oxygen-concentrations in white- and black-waters as well as contrasting water transparencies, and occur at mean maximum flood-levels of 7.5 and 9.0 m in the várzea and the igapó, respectively (Wittmann et al. 2010).

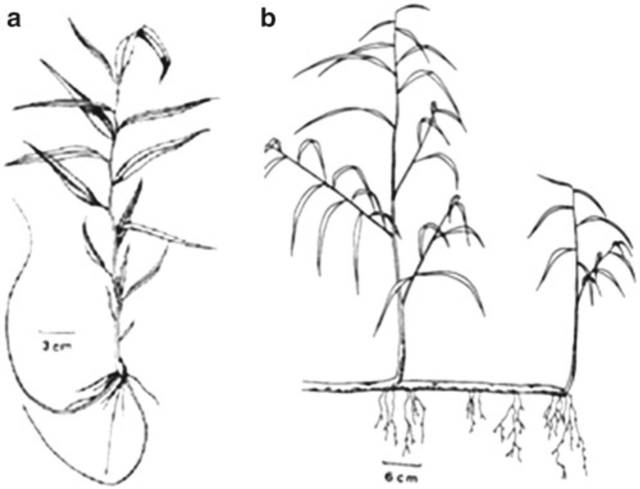

Fig. 13.5 Seedling (**a**) and vegetative sprout (**b**) of *Salix martiana* (Line drawings with kindly permission from Mareike Röder)

In várzea floodplains, erosive and depositional processes along the white-water rivers frequently create open areas for plant colonization and succession. The alluvial processes tend to keep riverine vegetation in different successional stages, and increase beta-diversity (Puhakka and Kalliola 1993). Pioneer species are favored by these local disturbances particularly during establishment because they profit from full light incidence, comparatively high nutrient status, and low competition, which enables them to grow fast (Johnson et al. 1976; Junk and Welcomme 1990). On freshly deposited sediment near the river channels, colonization by trees in central Amazonian várzea commonly starts with *Salix martiana* and *Alchornea castaneifolia* (Junk 1984; Wittmann et al. 2010). Besides formation of seedlings through the production of seeds, trees which are buried by constant sedimentation tend to produce sprouts by vigorous vegetative reproduction (Worbes et al. 1992; Wittmann and Parolin 2005, Fig. 13.5). Oliveira (1998) monitored the establishment of *Salix martiana* by both seeds and vegetative reproduction in two plots, each with the size of 230 m^2 above freshly deposited sediment at the Marchantaria Island, lower Solimões River, near the city of Manaus. Seedlings could easily be recognized by the reddish coloration of stalks and petioles. Height increase in 130 seedlings >40 cm averaged only 0.35 cm during a period of 15 days, whereas it averaged 0.8 cm in the same number of vegetatively regenerating sprouts during the same period. After 45 days of observation, seedlings reached heights of maximum 62 cm, whereas resprouting individuals reached heights of up to 130 cm (Fig. 13.6). Junk (personal communication) observed the impact of high sedimentation rates on the establishment of *Salix martiana* by excavating saplings of 50–80 cm in height. The primary roots were buried in the sediment up to >2 m depth. Every year, the river added 40–60 cm of new sediment during the aquatic phase and the saplings

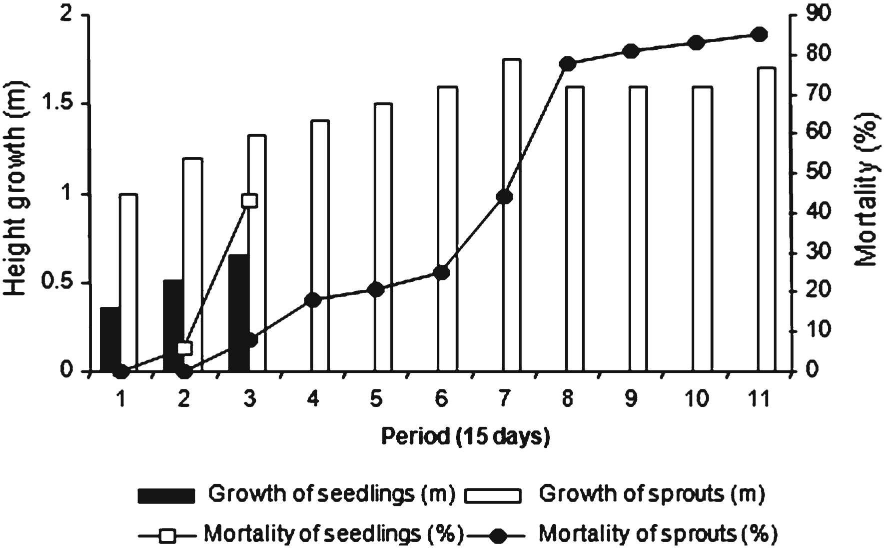

Fig. 13.6 Height growth and mortality in seedlings and vegetative sprouts from *Salix martiana*. Each interval in the x-axis represents an observation period of 15 days

reacted by developing new secondary root layer above the annual deposits to avoid asphyxia. This observation illustrates the difficulty of pioneer species to establish in these highly dynamic habitats.

In igapó forests, alluvial processes are less dynamic. The entire flooding gradient is generally covered by dense-canopy forest, and the colonization of open areas is restricted to small-scale gaps caused by mortality of single trees. Soil-nutrient levels are low, and newly established species may need several years until reaching autonomy, where reserves from attached seeds and hypocotyls are not longer required. Specific seed sizes and weights in igapó species are higher than in várzea species (Parolin 2000b). Large seeds are less subjected to physical disturbance by animals, damage by falling branches, litter or sediment layers, drought, darkness, and soil instability (Metcalfe and Grubb 1995; Grubb and Coomes 1997; Grubb 1998; Mack 1998; Kelly 1995). The generally larger seeds in nutrient-poor igapó are especially advantageous because they have more endosperm and are richer in energy reserves for the developing embryo (Moegenburg 1996), which enable seedlings to develop less dependent on soil nutrients (Parolin 2000b).

13.3.3 Establishment and Forest Succession

Amazonian floodplain forests are the most species-rich floodplain forests worldwide (Wittmann et al. 2006a), thus a huge variety of both, small-scale ecological niches and life-history traits can be expected among species. Most tree species are characterized by very restrict distribution along the flooding gradient (Junk 1989; Ayres 1993; Ferreira 1997; Wittmann et al. 2004), which can be explained by the degree of adaptations that were developed to tolerate the seasonal anaerobic site conditions (Junk et al. 2010b). According to the high beta-diversity of the alluvial landscape, different strategies of tree establishment can be observed, either linked to the flooding gradient and/or the forests' successional stage. Pioneer trees establish at highly flooded sites, and benefit from poorly shaded environments. As typical 'r-strategists' (Pianka 1970), they often produce large numbers of small and overall wind- or water-dispersed seeds, have fast growth rates and short life-cycles (Puhakka and Kalliola 1993, Worbes 1997). Establishment occurs during the short terrestrial phases and succeeds in monospecific stands, where seedling density can reach up to 1,000 individuals m^{-2} (e.g., *Cecropia latiloba*, Oliveira Wittmann et al. 2007b), and where total biomass of seedlings may amount to up to 13% of the aboveground wood biomass of trees ≥10 cm dbh in the same forest type (Schöngart 2003). However, seedling and sapling mortality is high when compared to individuals of later successional stages (Liebermann et al. 1985), and may amount to up to 99.98% Oliveira Wittmann et al. (2007b). In highly flooded sites, only a few individuals survive the first flooding persisting during the most part of the year. For this reason, sapling density of these species in general is low, and their success in establishment may be linked to consecutive years with exceptional low inundations, as observed, for example, during El Niño events (Wittmann and Junk 2003; Schöngart et al. 2004).

Late-successional species generally establish at higher topographic sites that are shaded by dense-canopy forest. With proceeding succession, influence of flooding and geomorphological dynamic decreases, because large stemmed and buttresses building trees establish, slowing water energy and favoring the deposition of fine grained sediment. The biogenic induced silting up results in sites which grow in topographic height (Wittmann et al. 2002b). Species richness of mature trees increases and forest physiognomy changes due to the establishment of large trees and the development of multi-layered stands. The more complex forest architecture in late-successional stages implies a high number of ecological niches at the seedling and sapling level, together with decreasing impact of flooding. Species richness and density of saplings increase, resulting in shade-tolerant species groups which establish under closed forest canopies, and in light tolerant species groups which establish near the forest borders and in gaps (Wittmann and Junk 2003; Assis 2008). Late-successional species in general produce comparatively low numbers of seeds, and use distinct and sometimes highly specialized dispersal strategies (Parolin et al. 2010b). Mortality rates, however, maybe strongly reduced in comparison to pioneer species (Oliveira-Wittmann et al. 2007b).

As many floodplain tree species in low flooded areas also occur in non-flooded environments (Wittmann et al. 2010), it is difficult to disentangle the complex interactions between genotypic species characteristics, flooding, and other environmental factors that may influence establishment in high-várzea trees. Conserva (2007) monitored growth and mortality of seedlings of ten várzea tree species over a period of 2 years at the Mamirauá Reserve, western Brazilian Amazon.

The results indicated that seedlings in a determined plot do not match the adult species of the same area and that seedlings are more likely immigrants originating from parent trees outside the investigated forest, owing to dispersal mechanisms. Although flooding in high várzea forests is less predictable as proposed by the ‘flood pulse concept’ (Junk et al. 1989), it implicates that late-successional species may disperse to long distances by flood waters even when not primarily hydrochoric. Investigating the population structure of four high-várzea tree species in the Mamirauá Reserve in dependence of mean flood height and duration, Marinho (2008) demonstrated that flooding events in these species occurred only 18 (*Guarea guidonia*), 23 (*Sterculia apetala*), 43 (*Hura crepitans*), and 48 times (*Ocotea cymbarum*), during the period of the last 100 years (historical data from the water gauge of the Negro/Amazon Rivers in Manaus). Mean flood height at the species populations, however, ranged from 8–168 cm, corresponding to flooded periods of 0–118 days year^{-1}. In relation to the distribution of adult trees (≥10 cm dbh), the distribution of saplings (≤10 cm dbh) was restricted to higher topographic areas in all investigated species. This illustrates that irregular flood conditions in high várzea forests may induce strong disturbance on the establishment of poorly flood-adapted species, and that the ‘physical escape’ from a submerged environment is an important acclimation in these tree species (Parolin 2000b, Voesenek et al. 2003).

13.4 Conclusions

The contact of diaspores with river waters when dispersing tends to accelerate germination and increase germination rates in buoyant seeds, whereas it deprives germination in submerged seeds. In both cases, the availability of atmospheric oxygen and light are crucial factors for germination.

Waterlogging in buoyant and submerged seeds does not shorten seed longevity, which can last up to ≥120 days in several species. Such seeds may persist for an entire aquatic phase and establish in the following terrestrial phase, a strategy which is beneficial in flood pulsing environments. In addition, some species with buoyant seeds develop seedlings while floating, but it remains unclear if this represents an advantage when seedlings land on substrate.

Despite the physiological stresses associated to the periodical inundations, seedlings of Amazonian floodplain trees perform very well during varying periods of submergence. Pioneer trees compensate high mortality rates by elevated productions of overall-dispersed seeds. Late-successional trees have lower reproduction rates, but in general also lower mortality rates.

The position of tree species along the flooding gradient promotes distinct establishment strategies: Species which occupy highly flooded environments tolerate submergence, while species occupying less flooded areas tend to avoid stress by the physical escape from submerged environments. In poorly adapted species, flooding represents disturbance particularly at the seedling level.

As young and small individuals frequently become completely submerged and undergo heavier flood stress than adult individuals, long-term field observations covering several terrestrial and aquatic phases are needed to better understand the impact of inundations on germination, establishment, growth and survival of tree populations of Amazonian floodplains.

Chapter 14
Nitrogen Balance of a Floodplain Forest of the Amazon River: The Role of Nitrogen Fixation

Jürgen Kern, Heidi Kreibich, Matthias Koschorreck, and Assad Darwich

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14.1 Introduction

The high biomass production in the várzea depends on a high supply of nitrogen, one of the most important macronutrients. There are three main paths for nitrogen to reach the floodplain. Nitrogen derives firstly from the water of the Amazon River

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when it inundates the floodplain during rising water, secondly from atmospheric deposition, and thirdly from biological N_2 fixation (Kern and Darwich 1997). Atmospheric N_2 is fixed in various ecotopes, primarily on high elevational ranges of the floodplain. At an elevational range of 22–25 m a.s.l. the forest under study is located on a ridge on Marchantaria Island. It is influenced by the water level of the Camaleão Lake, leading to an average inundation period between 4.7 and 7.6 months per year. In this most advanced successional stage of phytocoenoses, pathways of nitrogen input and output were studied next to Lake Camaleão on Marchantaria Island (Kreibich et al. 2006). This island is not affected hydrochemically by non-inundated upland (terra firme). Interpretation of the results are therefore restricted to exclusive white-water habitats of the central Amazon floodplain.

It already has been shown that legume-rhizobia symbioses are contributing to the N-balance of tropical floodplain forests (Martinelli et al. 1992; Barrios and Herrera 1994; Sprent 1999). However, there is little knowledge about the actual nitrogen gains, the seasonal variability of N fluxes and the mechanisms, which are responsible for gaseous nitrogen turnover within the várzea forest. Furthermore, it is not clear to what extent the nitrogen cycle is closed and how far the várzea forest also plays a role in nitrogen aquisition for ecotopes on lower stages in the várzea (Junk 1997b). The aim of this chapter is to assess the importance of symbiotic N_2 fixation for the nutrition of the várzea forest and to gain information for its sustainable use.

14.2 Nitrogen Sources on the Floodplain

14.2.1 River Water

The river water supplies a lot of nitrogen, at least to areas of low elevation. It contributes 70% to the total N input into a lake area of the floodplain (Kern and Darwich 1997) and 18–32% to the total N input to a forested area on Marchantaria Island (Kreibich and Kern 2004). The River Solimões/Amazon is an important nitrogen source feeding the várzea and its floodplain forest. At rising water, NO_3^- is the main nitrogen component with concentrations of up to 15 μmol l^{-1} imported from the river channel to the várzea lakes (Fig. 14.1). Conversely, with receding water the várzea lakes export more NH_4^+ than NO_3^- to the river (Kern and Darwich 1997). Besides dissolved nitrogen, particulate nitrogen (PN) from biogenic sources is exchanged between the River Solimões/Amazon and the floodplain. Taking an average value of 85 mg l^{-1} for total suspended solids (TSS), then the rising river water supplies about 11 μmol l^{-1} PN by this path (Engle and Melack 1993; Mertes 1994; Kern and Darwich 1997). Rising and receding water also means that parts of herbaceous and woody plants follow the water flow. Besides such passive impact of the flood pulse on the exchange of coarse organic material between the river channel and the floodplain, another process that is driven actively is the migration of fish. Although no detailed information exists about the nitrogen flux in terms of fish migration and fishing, highly structured littoral zones of the várzea offer a suitable habitat for spawning and for feeding of young fish (Junk et al. 1997). Therefore if the biotic component of the river water

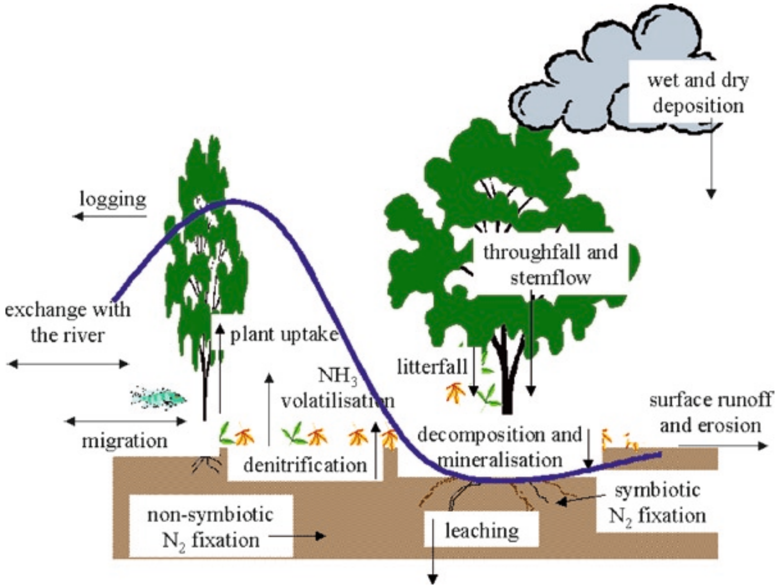

Fig. 14.1 Scheme of input and output N fluxes as well as internal N cycling in the várzea forest. The line reflects the flood pulse

is included in the considerations, it is reasonable to assume, that the várzea plays a much greater role as a source for fish protein than as a nitrogen sink.

Related to an inundation period of 4.7–7.6 months per year, the total abiotic nitrogen input via the river can be calculated to range between 4.4 and 10.5 kg N ha^{-1} $year^{-1}$. Nitrogen output from the várzea to the river due to re-suspension of sediments and outflow of dissolved nitrogen accounts for 6.0 kg N ha^{-1} $year^{-1}$ (Kern and Darwich 1997).

14.2.2 Atmospheric Deposition

Another pathway taken by nitrogen is dry, wet and occult deposition (Fig. 14.1). Nitrogen compounds such as ammonium and nitrate, which derive from atmospheric deposition, range between 2 and 5 kg N ha^{-1} $year^{-1}$ in the Amazon region, as reported by Kern and Darwich (1997) and Fabian et al. (2005). Most nitrogen oxides and the other nutrients in the atmosphere of the Amazon region are deposited in the biosphere by wet deposition. Dry deposition of nitrogen plays only a minor role (Lesack and Melack 1991).

The quantity and quality of the Central Amazon precipitation are subject to spatial and temporal variability (Ribeiro and Adis 1984; Lesack and Melack 1991; Kern 1995). In the várzea at Lake Camaleão, inorganic N concentrations (NH_4^+ and NO_3^-) of rain ranged up to 30 µmol N l^{-1}, yielding a deposition rate of 2.6 kg N ha^{-1} $year^{-1}$ (Kern and Darwich 1997).

Important aspects of local and global atmospheric N budgets also include organic forms of nitrogen deposition from the atmosphere. The contribution of organic N to total N loading varies from site to site, but is consistently around 30% of the total N load (Neff et al. 2002). Cornell et al. (2003) reported that some of the organic material observed does not seem to be locally generated. Possible sources of atmospheric N deposition include the long-range transport of dust, pollen, bacteria and NO_x gases. Nitrogen found in dry and wet deposition may derive from biomass burning, which is suspected to enhance nitrate input even to pristine natural forest environments. Fabian et al. (2005) traced the atmospheric nitrogen depositions of up to 4.4 kg NH_4-N ha^{-1} $year^{-1}$ and 0.8 kg NO_3-N ha^{-1} $year^{-1}$ in the mountainous rain forest of south Ecuador back to forest fires far upwind from the Amazon basin. Additional N deposition due to anthropogenic sources may affect the ecosystem and its biodiversity. Plant growth in the várzea may be stimulated because other nutrients such as P, K and Ca are sufficiently supplied by the flooding river water, by contrast with weathered soils of tropical upland forests where these nutrients are suggested to be limited (Matson et al. 1999).

14.2.3 N_2 Fixation

Although the river water is rich in major solutes, the N requirement for net primary production of annual and perennial vegetation is not met by the input of river water and atmospheric deposition (Furch 1997; Kern and Darwich 1997). Therefore, the utilization of atmospheric N_2 as a supplemental N source must be taken into account, provided that nitrogen flux is not restricted to a closed cycle. N_2 fixation has already been described for the várzea by Salati et al. (1982); Melack and Fisher (1988); Martinelli et al. (1992); Doyle and Fisher (1994); Kern (1995) and Kreibich et al. (2006). All forms of N_2 fixation with a transition from free living N_2 fixers to obligatory symbioses found in leguminosae occur in the várzea. Besides the floodplain forest where Kreibich et al. (2006) found considerable N input by N_2 fixation, it is suggested that the root-periphyton complex of aquatic macrophytes is a hotspot of gaseous N flux within the várzea.

According to the rates of periphytic N_2 fixation, the atmospheric nitrogen source is most important for the floating stands of *Paspalum repens* with contributions to plant N of up to 90% (Kern and Darwich 2003). It may be concluded that fixation of atmospheric N_2 is a successful adaptive strategy to avoid N limitation in the stands of macrophytes, which cover a very dynamic ecotone at low to medium elevational boundaries within the várzea. By means of a lake input-export budget for total N, it could be shown that about 8% and 17% were derived respectively from N_2 fixation at Lake Calado (Doyle and Fisher 1994) and at Lake Camaleão (Kern and Darwich 1997). Although stands of floating macrophytes are often lost from the várzea by heavy floods and the river current, a part of the organic macrophyte material is deposited within the floodplain forest and thereby contributes to increasing productivity.

Table 14.1 Plant family importance level of woody species resulting from the sum of relative richness, relative density and relative dominance of the eight most important plant families found next to Lake Camaleão, listed in order of their importance

Plant families	Relative richness (%)	Relative density (%)	Relative dominance (%)	Family importance level
Capparaceae	2	37	20	59
Verbenaceae	2	23	29	54
Leguminosae	27	10	10	47
Flacourtiaceae	5	7	6	18
Tiliaceae	2	2	12	16
Bombacaceae	2	2	10	14
Myrtaceae	2	7	2	11
Euphorbiaceae	7	3	1	11
Remaining 17 families	50	9	10	69

Most woody species in the flooded forest at Lake Camaleão belong to the leguminosae family (Table 14.1). First data on the fixation potential of semi-terrestrial leguminosae in the várzea have been reported by Sylvester-Bradley et al. (1980) and Magalhães (1986). Indications of N_2 fixation within the floodplain forest are given by low $\delta^{15}N$ values in the leaves of perennial herbaceous and woody leguminosae (Kern et al. 2000; Kreibich 2002; Kreibich et al. 2006).

14.3 Symbiotic N_2 Fixation of the Floodplain Forest

14.3.1 Legumes

Besides the occurrence of lianas and some aquatic macrophytes, trees dominate the leguminosae plant family, which is the richest family of tree species in the várzea (Worbes 1997). Thus, there might be a high potential for symbiotic N_2 fixation. However, low or absent symbiotic N_2 fixation of woody legumes was reported by Salati et al. (1982), Yoneyama et al. (1993), Högberg and Alexander (1995), Thielen-Klinge (1997) and Roggy et al. (1999a). It has been suggested, that in tropical primary forests, nodulation might be repressed by organic substances from the vegetation, e.g. tannins (Moreira et al. 1992), but abundant nodulation of seedlings and young trees in these forests might rather indicate a strong influence of the plant age as reported by Norris (1969). Additionally, it is believed that N_2 fixation of nodulated legumes is more important in disturbed areas compared to forests (Faria et al. 1984; Sprent 1987). For example, Gehring and Vlek (2004) reported high symbiotic N_2 fixation throughout the 2–25 years of secondary forest regrowth after slash-and-burn land-use, but low or negligible fixation in their primary forest sites in central Amazonia. This is explained by relatively high abundance of N and efficient internal N cycling in terra firme climax forests, as well as prevalent phosphorus limitation of these ecosystems as mentioned in Section 14.2.2

(Martinelli et al. 1999; Sprent 1987; Vitousek 1984). Thus, the nutrient status of the soil is another important factor influencing symbiotic N_2 fixation. High mineral N concentrations generally reduce or even inhibit root nodule formation (Tsai et al. 1998), while good supply with other nutrients, especially potassium, has a positive effect on symbiotic N_2 fixation and may improve plant resistance to environmental stress (Sangakkara et al. 1996).

The importance of symbiotic N_2 fixation for the nutrition of the várzea forest was assessed by monitoring N_2 fixation for 20 months during two hydrological cycles. The maximum water level during the study period was 29.5 m a.s.l.; the lowest spot of the study area was then flooded by 7.5 m. The time from October to February, when the forest soil was exposed to air, was considered as the terrestrial period in contrast to the aquatic period between March and September, when the forest soil was inundated. Transition periods were in September/October and February/March. The study area is 1.5 km long and between 80 and 120 m wide (approximately 15 ha).

In a stand structure analysis, 1,441 woody plants were inventoried in four plots (total area: 2.1 ha). In total, 44 woody species from 25 families were determined. Among the legume trees 22 individuals belonged to the Caesalpiniodeae, 74 to the Papilionoideae and 47 to the Mimosoideae families. This means that legumes had an average absolute density of 68 individuals per hectare.

Twenty-four legume species were found in the study area, of which 12 belonged to the Papilionoideae, six to the Caesalpiniodeae and six to the Mimosoideae families. Ten species were trees, five shrubs, six woody climbers, two herbs and one an aquatic plant (Table 14.2). Twenty-one of all legume species (88%) in the study area were nodulated and only three were non-nodulated. The most important legume species in the study area were the liana *Dalbergia riparia* (Papilionoideae) and the trees *Macrolobium acaciifolium* (Caesalpiniodeae), *Albizia multiflora* (Mimosoideae) and *Pterocarpus amazonum* (Papilionoideae). For the first time in Brazil nodules could be observed on a species of *Pterocarpus* (Kreibich 2002). There is no literature report about the nodulation status of the genus *Cymbosema*, but since this genus belongs to the tribe Phaseoleae, which contains predominantly nodulated genera/species (Faria et al. 1989), *Cymbosema roseum* was treated as a nodulated species. A further indication of its nodulation is its low $\delta^{15}N$ value (Section 14.3.3, Fig. 14.3).

14.3.2 Bacterial Symbionts

Rhizobia nodulating tropical legumes show a high biodiversity, including fast and slow growing strains (Haukka et al. 1996, 1998; Lafay and Burdon 1998; Doignon-Bourcier et al. 1999). Isolates from legume plants from the Amazon region were found to belong to the genera *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium* and *Sinorhizobium* (Moreira et al. 1993; Moreira et al. 1998). Growth rates can already be used as a rough indication of the genus to which a nodule isolate might belong (Jordan 1984). In the study by Kreibich (2002), a molecular genetic

Table 14.2 Characterisation of the legume species identified in the study area

Species	Sub-family	Growth habit	[a]Wood-density (g cm^{-3})	[b]Leaf periodicity	Leaf N content (%)	[c]Nodulation status
Acosmium nitens	Caes.	Tree	0.74	Deciduous	ND	+
Aeschynomene sp.	Papil.	Shrub	ND	ND	4.7	+
Albizia multiflora	Mimos.	Tree	0.62	Deciduous	3.9	+
Bauhinia sp.	Caes.	Shrub	ND	ND	4.4	–
Campsiandra comosa	Caes.	Tree	0.81–0.86	Deciduous	2.2	+
Chamaecrista sp.	Caes.	Tree	ND	ND	2.7	+
Crudia amazonica	Caes.	Tree	0.87	Deciduous	2.8	–
Cymbosema roseum	Papil.	Woody climber	ND	ND	3.6	(+)
Dalbergia inundata	Papil.	Woody climber	0.75–1.00	ND	2.7	+
Dalbergia riparia	Papil.	Woody climber	0.75–1.00	ND	3.0	+
Entada polyphylla	Mimos.	Shrub	ND	ND	4.2	+
Inga splendens	Mimos.	Tree	ND	ND	3.8	+
Lonchocarpus sp.	Papil.	Woody climber	0.70–0.95	ND	2.4	+
Machaerium aristulatum	Papil.	Woody climber	0.70	ND	2.3	+
Machaerium ferox	Papil.	Woody climber	0.70	ND	ND	+
Macrolobium acaciifolium	Caesalp.	Tree	0.43–0.56	Semi-deciduous	2.6	–
Mimosa pigra	Mimos.	Shrub	ND	Deciduous	3.5	+
Neptunia oleracea	Mimos.	Aquatic plant	ND	ND	3.8	+
Pterocarpus amazonum	Papil.	Tree	0.33–0.40	Deciduous	2.8	+
Sesbania exasperata	Papil.	Shrub	ND	ND	5.3	+
Swartzia sp.	Papil.	Tree	0.63–0.86	Evergreen	2.4	+
Teramnus volubilis	Papil.	Herb	ND	ND	3.8	+
Vigna sp.	Papil.	Herb	ND	ND	3.9	+
Zygia inaequalis	Mimos.	Tree	0.72	Evergreen	2.6	+

[a] Wood-density data are published by Allen and Allen (1981), Worbes et al. (1992), Fearnside (1997) and Parolin et al. (1998)

[b] Leaf periodicity data are published by Klinge et al. (1983) and Schöngart et al. (2002)

[c] Nodulation status given by Allen and Allen (1981), Faria and Lima (1998), Faria et al. (1984, 1987, 1989) and Sprent (1995)

ND – not determined and no literature data available approach was chosen for the characterisation of rhizobia biodiversity and possible symbioses with legume species. For the formation of an effective symbiosis, rhizobia require several classes of symbiosis-relevant genes (Niner and Hirsch 1998). These include *nod* genes, which encode for enzymes involved in *nod*-factor biosynthesis (Broughton et al. 2000) that stimulate the plants to produce symbiotic nodules, and the nitrogenase structural and regulatory *nif* genes (Haukka et al. 1998). The *nod* genes are unique to rhizobia, whereas *nif* genes are found in all N_2 fixing bacteria (Young and Haukka 1996). In the várzea forest under study, altogether 18 isolates which exhibited typical rhizobial colony and cell morphology were obtained. The 14 isolates from *Albizia multiflora* and four isolates from *Pterocarpus* all had *nod* as well as *nif* gene regions, which were amplified with the *nod*C and *nif*DK primers, respectively. The presence of both *nod* and *nif* genes in the isolates from the two legume trees is a strong indication that these isolates are rhizobia.

The 18 isolates can be grouped in two major clusters that most likely correspond to at least two different genera and species, based on their linkage level (Fig. 14.2). Host specificity of rhizobia is a well known phenomenon, but it does not necessarily lead to

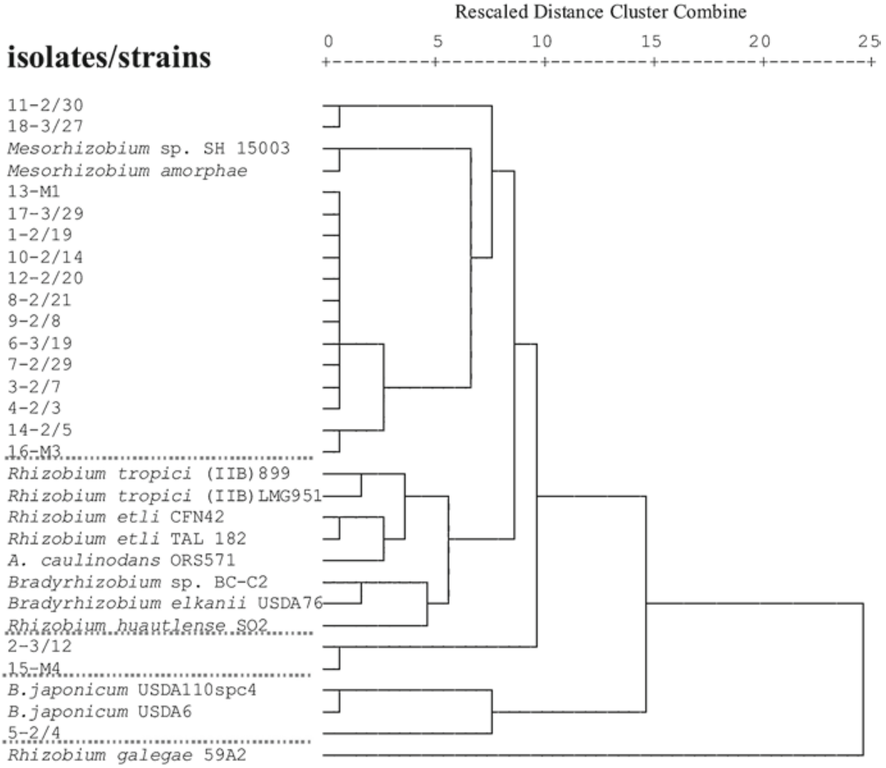

Fig. 14.2 Cluster analyses of combined *Dde*I, *Hha*I, *Msp*I and *Sau*3AI restriction patterns of amplified 16S rDNA. Empirical RFLP patterns of all isolates and theoretical RFLP patterns of 13 reference strains were included

a correlation between genotypic clusters obtained and the divergence groups of legumes from which the strains were isolated (Moreira et al. 1993; Haukka et al. 1998; Kreibich 2002). Despite some uncertainties in analysing the diversity of the isolates at stricter taxonomic resolution, rep-PCR genomic fingerprinting with the GTG_5 primer resulted in *Mesorhizobium* as the main genus nodulating *Albizia multiflora* and *Pterocarpus amazonum* on Marchantaria Island. This is remarkable because in most cases *Bradyrhizobium* strains are known to nodulate tropical legumes (Norris 1965; Jordan 1984; Moreira et al. 1993; Lafay and Burdon 1998; Vinuesa et al. 1998; Doignon-Bourcier et al. 1999). However, at least partial 16S rDNA sequencing of representatives of each of the five genotypes detected in this study would be required to classify the corresponding isolates at the genus to species levels of taxonomic resolution.

In summary, the genotypic diversity of nodulation rhizobia is remarkable, considering the small isolate collection analysed. Thus, highly adapted bacteria species are believed to be present in the várzea under study. Specific nodulation of legume species might be one response to the adverse conditions within the aquatic terrestrial transition zone.

14.3.3 Isotopic ^{15}N Analyses to Estimate N_2 Fixation

Nitrogen occurs in different isotopes (^{14}N and ^{15}N) in biotic and abiotic environments. Since atmospheric nitrogen is depleted in ^{15}N, N_2 fixation results in lower isotopic ratios of $^{15}N/^{14}N$ compared to the uptake of soil nitrogen. Furthermore, fractionation processes during N uptake affect the isotopic contents of ^{14}N and ^{15}N and thus the ^{15}N content within one plant. In order to assess the extent of nitrogen in legumes derived from atmosphere (Ndfa), the ^{15}N natural abundance method has been established (Shearer and Kohl 1986, 1988). The ^{15}N natural abundance is expressed as δ unit in per mil (‰):

$$\delta^{15}\mathrm{N} = \frac{(\mathrm{atom}\%^{15}\mathrm{N})_{\mathrm{sample}} - (\mathrm{atom}\%^{15}\mathrm{N})_{\mathrm{standard}}}{(\mathrm{atom}\%^{15}\mathrm{N})_{\mathrm{standard}}} * 1000 \tag{14.1}$$

The international standard is atmospheric N_2 with a ^{15}N atom% of 0.3663. The percentage of N derived from the atmosphere (%Ndfa) was calculated according to Shearer and Kohl (1986) and Yoneyama et al. (1993) as:

$$\%\mathrm{Ndfa} = \frac{\delta^{15}\mathrm{N}_{\mathrm{R}} - \delta^{15}\mathrm{N}_{\mathrm{F}}}{\delta^{15}\mathrm{N}_{\mathrm{R}} - \delta^{15}\mathrm{N}_{\mathrm{A}}} \tag{14.2}$$

with

$\delta^{15}N_F$ = $\delta^{15}N$ natural abundance of the potentially N_2 fixing target plant

$\delta^{15}N_R$ = $\delta^{15}N$ natural abundance determined using a single or a mixture of non-N_2 fixing reference plants. These approaches yielded a minimum reference value of 4.0‰ and a maximum reference value of 7.1‰ for the study area

$\delta^{15}N_A$ = δ^{15}N natural abundance of fixed N, which was determined to be −4.9‰, with legumes from the várzea forest grown without soil N

The average percentage of plant N, which derives from the atmosphere for the várzea forest, was estimated via the combination of the %Ndfa results of the single legume species with their respective important value indexes (IVI) resulting from a stand structure analysis (Section 14.3.1). For the non-nodulated species the %Ndfa was set at zero, and for the nodulated legumes minimum and maximum %Ndfa values were taken to calculate the two possible extremes. Depending on the IVI of the species, the weighted average %Ndfa for the forest was calculated as follows:

$$\text{weighted average \% Ndfa} = \frac{\sum_{i=1}^{n} \%\text{Ndfa}_i \bullet \text{IVI}_i}{\sum_{i=1}^{n} \text{IVI}_i} \tag{14.3}$$

Plants of all growth habits, from aquatic plants to trees, are characterised by δ^{15}N values found between −1.4‰ and 6.8‰ (Fig. 14.3). Mean δ^{15}N values of the legumes and the non-legumes under study are 1.4‰ and 4.6‰, respectively. Although δ^{15}N values of both groups overlap, δ^{15}N values of the legumes are significantly lower by comparison with the non-legumes. That applies to the N contents of legumes too, which are significantly higher ($p < 0.05$). Mean N content in leaves of the legume plants is 3.3%, and in the non-legumes it is 2.5%, indicating better nutrition and higher requirements of legumes, respectively. For most species isotope data correlated well with nodulation.

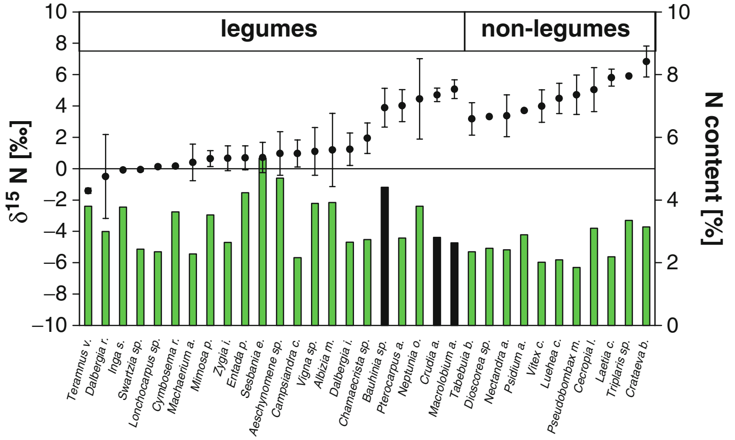

Fig. 14.3 Mean δ^{15}N values (*points*) with their standard deviations and mean N contents (*columns*) of all woody and non-woody species investigated, organised according to legumes/non-legumes and increasing δ^{15}N values (From Kreibich et al. 2006). Black bars represent those legumes without nodulation

The three non-nodulated legumes *Bauhinia* sp., *Crudia amazonica* and *Macrolobium acaciifolium* are in the same range as the values of non-legumes found in the várzea and in other regions of Brazil (Yoneyama et al. 1993). A similar pattern is found in the legume tree *Pterocarpus amazonum*. Even N_2 fixing activity could be measured in the nodules, but scarce nodulation by contrast with *Campsiandra*, *Albizia* and *Zygia* seems to be the reason for the low input of fixed N_2 yielding high $\delta^{15}N$ values.

Some non-legumes have relatively low $\delta^{15}N$ values similar to those of the legumes. One explanation might be their different ecological behaviour. Different rooting depths and mycorrhizal infection are considered to have an effect on the $\delta^{15}N$ values of plants (Högberg 1990; Roggy et al. 1999b). Of the tree species in the várzea, 81% have vesicular-arbuscular mycorrhizal symbioses (Meyer 1991; Meyer et al. 2010). For instance, the roots of *Tabebuia barbata*, the non-legume with the lowest $\delta^{15}N$ value, show a high density of intercellular hyphae and vesicles in contrast to *Crataeva benthamii* with no mycorrhiza and the highest $\delta^{15}N$ value. This kind of symbiosis seems to improve soil N uptake, accompanied by isotope fractionation and selective uptake of ^{14}N.

The mean %Ndfa values of the woody and non-woody nodulated legumes range between 9% and 66% (Table 14.3), similar to the results of Yoneyama et al. (1993) who reported values from negligible to 80% Ndfa for tropical plants in Thailand. More than half of the nodulated legume species under study have %Ndfa values

Table 14.3 Percentage of Ndfa of nodulated species in the study area calculated with four different reference plants between 4.0‰ and 7.1‰ and the average of the four reference plants given as mean (Kreibich 2002; Kreibich et al. 2006)

Nodulated legume species	Number of plants	$\delta^{15}N$ (‰)	Ndfa (%)		
			Mean	Minimum	Maximum
Teramnus volubilis	3	−1.4 ± 0.2	66	63	70
Dalbergia riparia	5	−0.5 ± 2.7	57	54	62
Inga splendens	1	−0.1	53	49	59
Swartzia sp.	2	−0.1 ± 0.1	53	49	59
Lonchocarpus sp.	2	0.1 ± 0.1	51	47	57
Cymbosema roseum	1	0.2	51	47	57
Machaerium aristulatum	3	0.4 ± 1.2	49	44	55
Mimosa pigra	7	0.6 ± 0.5	47	42	53
Entada polyphylla	3	0.7 ± 0.8	46	41	52
Sesbania exasperate	3	0.7 ± 1.0	46	41	52
Zygia inaequalis	10	0.7 ± 0.8	45	41	52
Aeschynomene sp.	2	1.0 ± 1.4	43	38	50
Campsiandra comosa	2	1.0 ± 0.9	43	38	50
Vigna sp.	4	1.1 ± 1.5	42	37	49
Dalbergia inundata	5	1.2 ± 1.0	41	35	48
Albizia multiflora	16	1.2 ± 2.3	39	31	48
Chamaecrista sp.	4	1.9 ± 1.0	34	28	42
Pterocarpus amazonum	11	4.0 ± 1.0	14	6	24
Neptunia oleracea	3	4.5 ± 2.6	9	2	20

over 45%. The estimated average %Ndfa of 4–5% of the várzea forest is remarkable, since other studies reported negligible N_2 fixation of woody legumes and low or absent symbiotic N_2 fixation in tropical forests (Roggy et al. 1999a; Högberg and Alexander 1995; Thielen-Klinge 1997; Salati et al. 1982; Yoneyama et al. 1993; Shearer and Kohl 1986).

On Marchantaria Island large intraspecific variation of $\delta^{15}N$ values reflects the facultative process of N_2 fixation. Plant species are able to use both atmospheric N with low $\delta^{15}N$ and soil N with relatively high $\delta^{15}N$. Generally, the variability in $\delta^{15}N$ values between individual trees of one species is due to site effects, plant conditions and differences in N_2 fixation. Factors influencing N_2 fixation are micro-symbiont efficiency, plant condition and soil properties such as pH, moisture content, temperature, and nutrient availability (Williams et al. 1988).

Generally, low O_2 concentrations, which occur during flooding, reduce root growth and alter root N metabolism significantly. However, sensitivity to low O_2 concentrations is quite variable between legume species and has been answered by different strategies to periodical flooding. Pressurised or diffusive gas transport is one example (Grosse et al. 1996; Haase et al. 2003, see Haase and Rätsch 2010) and may support sufficient O_2 supply to the root system and probably also maintain symbiotic N_2 fixation during flooding. This may be one reason, why most tree species do not show significant seasonal variation in their $\delta^{15}N$ values (Kreibich et al. 2006). This means that N_2 fixation within the Legume/Rhizobium symbiosis is not affected by changing water levels. In contrast to this, the non-symbiotic N_2 fixation in the surface layer of the forest soil shows a clear seasonal pattern with an input of 3.6 kg N ha^{-1} during the terrestrial phase and 0.5 kg N ha^{-1} during the aquatic phase (Kreibich and Kern 2003).

14.4 Availability and Fate of Nitrogen

14.4.1 Plant Availability

Organic nitrogen and its products of mineralisation, ammonium and nitrate, are the major nitrogen compounds available for microbial conversion and plant uptake. In the river channel NO_3^- is the predominant dissolved N compound, in contrast to the floodplain lakes where dissolved organic N and NH_4^+ occur at high concentrations as shown for Lake Camaleão (Kern 1995). Different hydrochemical properties are due to different oxygen supplies in the river and the várzea that result in different nitrification rates. This means that the intensity of nitrification is linked with other oxygen producing and consuming processes such as the decomposition of organic material, which is proceeding at high rates within the várzea (Piedade et al. 1991; Furch and Junk 1992; Darwich et al. 2000).

During low water when the forest soil is exposed to air, nitrogen may undergo rapid transformation in the soil, increasing the availability and uptake by terrestrial plants. Plant uptake seems to be the main process consuming N from soil during the terrestrial phase. This corresponds with the high nutrient requirement in the várzea forest, which is reflected by high biomass production, mainly occurring during the terrestrial phase (Worbes 1985). On a yearly basis about 292 kg N ha^{-1} are needed for the biomass production of the aboveground forest (Furch 1997). This amount exceeds the consumption of NH_4^+ during the terrestrial phase many times and reflects the high turnover of N.

Ammonium is always the dominant form of inorganic nitrogen at about one order of magnitude higher than NO_3-N. In the upper soil layer, ammonium increases during the terrestrial phase and is highest during the aquatic phase (Fig. 14.4a). This is probably caused by mineralisation of organic material in the litter layer, which is built up by leaf litter fall yielding about 155 kg N ha^{-1} $year^{-1}$ (Furch and Klinge 1989). Thus the soil N pool is permanently replenished by decomposition of organic matter.

Both ammonium and nitrate contents decrease significantly with soil depth (Fig. 14.5). Assuming a mineralisation capacity of 1% for total N in the soil layer 0–20 cm, 36 kg N ha^{-1} enrich the soil NH_4^+ pool per year. Besides plant uptake, nitrification was most likely responsible for consumption of NH_4^+. Since soil water content is one of the main factors regulating nitrification (Bollmann and Conrad 1998),

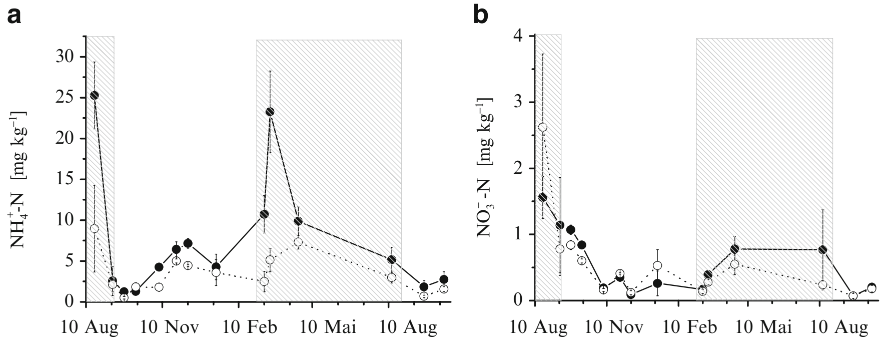

Fig. 14.4 Extractable ammonium (**a**) and nitrate (**b**) in the forest soil during one hydrological cycle 1996–1997 (● – 0–1 cm, ○ – 1–10 cm). The shaded areas mark the flooded period (N = 3)

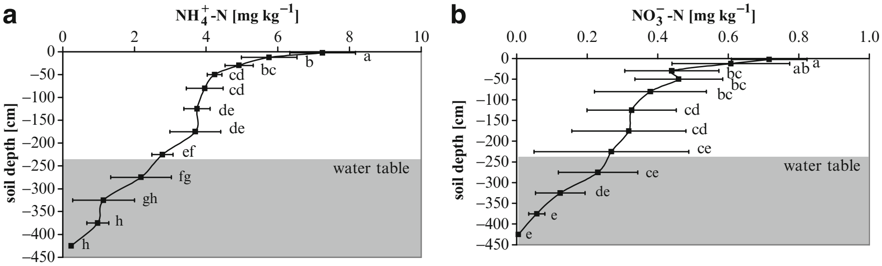

Fig. 14.5 NH_4^+-N (**a**) and NO_3^--N (**b**) content in the soil profile, measured in October 1999 (n = 3; mean and standard deviation). Soil below the water table (230 cm depth) is shaded grey, points followed by the same letter are not significantly different by $p < 0.05$)

oxidation of NH_4^+ may be favoured due to the O_2 supply during the terrestrial phase. An accumulation of NO_3^- due to nitrification during the terrestrial phase, however, could not be observed. This is pointing to plant uptake and a potential for denitrification, which always exceeded the nitrification rate.

As shown by Kreibich (2002), the average total N decreased with soil depth from 9.8 g kg^{-1} in litter to 0.7 g kg^{-1} at 60–100 cm depth (Table 14.4) and there was only little seasonal variation in total N (Koschorreck and Darwich 2003). Average C content displayed a similar trend with a high value of 196.7 g kg^{-1} in litter, decreasing to 5.8 g kg^{-1} at a depth of 60–100 cm. Also the C/N ratio decreased with soil depth; in litter it was highest at 19.9 and significantly different from the mineral soil.

14.4.2 Leaching

In Amazonia the main part of dissolved inorganic nitrogen (DIN) in floodplain soils is NH_4^+-N, by contrast with upland soils, where DIN is predominated by NO_3^--N (Neill et al. 1999). Since NO_3^- is a very mobile ion, it is predestined to be leached from the soil. However, besides NO_3^-, NH_4^+ may also be affected by the transfer to deeper soil layers (Furch 1997), leading to an increase in NH_4^+ concentrations in the adjacent lake water. Seepage as observed for major cations (Furch 1999; Cullmann et al. 2006) probably also plays a considerable role for nitrogen transport, although difficult to quantify due to microbial conversion and gaseous N emissions. During receding water or rainfall, leaching may play an important role in the displacement of N. This may be true particularly in stands of N_2 fixing legumes, which on the one hand enhance the N supply and its uptake, as reflected by high N contents of *A. multiflora* leaves (38 g N kg^{-1}) by comparison with *T. barbata* leaves (23 g N kg^{-1}). On the other hand it could be shown that nitrogen was leached from the forest soil within the rhizosphere of the frequently found tree species *Albizia multiflora*. By means of resin cores according to Bischoff et al. (1999) and Lehmann et al. (2001), leaching rates were measured under legume trees and non-legume trees during 4 months of one terrestrial phase (Kreibich et al. 2003). The resin cores were installed at a soil depth of 20 cm, which is considered as the root zone most responsible for nutrient uptake. Close to the legume trees the N flux was significantly higher than close to the non-legume trees ($p < 0.05$). In the rhizosphere of *A. multiflora,* on average 3.8 kg N ha^{-1} were lost by leaching. This amount was two to three times higher than the loss close to *T. barbata* and the loss at the control sites (Table 14.5). However, all these leaching rates are low compared with European forest soils, where annual leaching rates ranged between 13 and 81 kg N ha^{-1} $year^{-1}$ (Persson et al. 2000). Therefore a very efficient root uptake of available mineral nitrogen synchronised and synlocalised with the plant N demand can be assumed in the soil of the várzea forest.

Table 14.4 Chemical soil properties during the terrestrial period (mean ± standard deviation)

Depth (cm)	NO_3^--N (mg kg^{-1})	NO_2^--N (mg kg^{-1})	NH_4^+-N (mg kg^{-1})	Total N (g kg^{-1})	Total C (g kg^{-1})	C/N-ratio
Litter	1.5 ± 1.9	0.02 ± 0.02	8.9 ± 15.6	9.8 ± 3.1	196.7 ± 76.2	19.9 ± 3.9
0–5	0.7 ± 0.1	0.02 ± 0.02	7.3 ± 0.9	2.5 ± 0.9	32.5 ± 14.3	14.0 ± 10.7
5–20	0.6 ± 0.1	0.02 ± 0.02	5.8 ± 0.7	1.3 ± 0.3	13.0 ± 4.2	10.1 ± 2.0
20–40	0.4 ± 0.1	0.03 ± 0.03	4.9 ± 0.4	0.8 ± 0.2	8.4 ± 3.1	10.8 ± 4.1
40–60	0.5 ± 0.1	ND	4.2 ± 0.2	0.8 ± 0.2	5.3 ± 1.4	7.2 ± 0.7
60–100	0.4 ± 0.2	ND	4.0 ± 0.5	0.7 ± 0.4	5.8 ± 4.7	7.7 ± 2.0

Table 14.5 Leaching of NH_4^+-N and NO_3^--N ($N_{min} = NH_4^+$-N and NO_3^--N) at 20 cm depth under two native tree species by comparison with soil without vegetation in the várzea forest of the Central Amazon obtained by resin cores over a period of 132 days (means and standard errors; n = 4). Values in one column followed by the same letter **(a, b)** are not significantly different at $p < 0.05$ (From Kreibich et al. 2003)

	Leached nitrogen (kg N ha^{-1})		
Sites	NH_4^+-N	NO_3^--N	N_{min}
Albizia multiflora	$2.4_a \pm 1.2$	$1.3_a \pm 0.6$	$3.8_a \pm 1.3$
Tabebuia barbata	$0.8_b \pm 0.1$	$0.4_a \pm 0.2$	$1.2_b \pm 0.2$
Control	$0.9_b \pm 0.2$	$0.5_a \pm 0.3$	$1.4_b \pm 0.5$

The letters a and b are statistical indicators as in Fig. 14.5. They are not the same as in Fig. 14.2

14.4.3 Denitrification

First insights into the extent of nitrogen loss via denitrification along the aquatic/terrestrial transition zone on the Amazon floodplain were derived from studies at Lake Camaleão by Kern et al. (1996). Denitrification, the reduction of NO_3^- to N_2O and N_2, is the best known process besides nitrification and volatilisation, which releases nitrogen to the atmosphere. However, other microbiological pathways such as anaerobic ammonium oxidation (ANAMOX: $NH_4^+ + NO_2^- \rightarrow N_2$) may occur, which has been found during recent years to play a role in the release of gaseous N compounds (Graaf et al. 1995; Jetten et al. 1999; Haaijer et al. 2007). The release of gaseous nitrogen compounds not only means a nitrogen loss for the biosphere, but with its trace gases N_2O, NO and NO_2 it also contributes to the greenhouse effect and to stratospheric O_3 depletion, (Smith et al. 2003; Garcia-Montiel et al. 2004; Dick et al. 2006). Particularly water table fluctuations, as they occur periodically in Amazonian floodplains, play an important role in the release of nitrogen oxides. The transition of an aquatic phase to a terrestrial phase may be linked with desiccation and bacterial mortality and is thus suggested to be an important factor controlling the release of N_2 and N_2O (Koschorreck 2005). Oxygen as an electron acceptor and carbon as an electron donor play the key roles in the emission of N_2 and N_2O. Other factors are less important because NO_3^- concentrations are very low in flooded and exposed sediments, and pH values are high enough to let denitrification run mainly to N_2. A considerable loss of nitrogen in the entire unforested exposed sediment at Lake Camaleão has been reported (Kern and Darwich 1997; Koschorreck 2005). This nitrogen flux has to be assessed as quite high compared with those from the flooded forest and the terra firme forest (Jordan et al. 1983). It was shown that within the várzea forest at Lake Camaleão denitrification, measured after inhibition of the N_2O-reductase by acetylene, only occurs above a water content of 34% (Kreibich and Kern 2003). That would result in a loss of 1.6 kg N ha^{-1} considering the soil layer 0–5 cm during the terrestrial period of 1998. The aquatic period resulted in an N loss of 10.9 kg N ha^{-1}.

A measure of potential denitrification in the forest soil is given in Fig. 14.6a by the denitrifier enzyme activity (DEA), which is measured as N_2O increase in nitrate and glucose amended soil samples according to Koschorreck and Darwich (2003). In the floodplain forest soil DEA was higher during the aquatic phase. This can be explained by more reduced conditions and a supply of nitrate from the river water

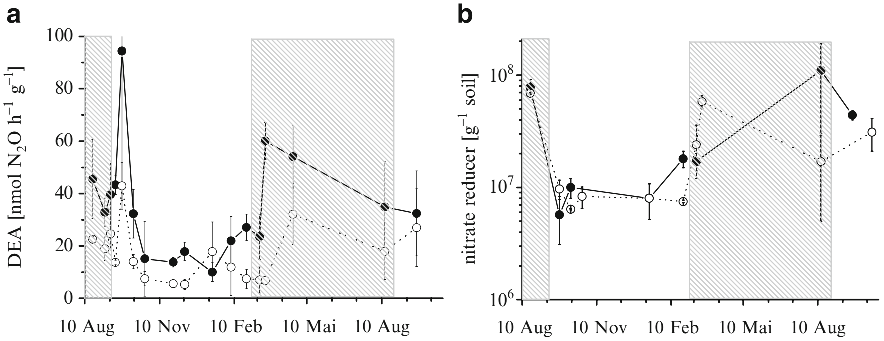

Fig. 14.6 Denitrifier enzyme activity (**a**) and MPN counts of nitrate reducing bacteria (**b**) in the várzea forest soil during one hydrological cycle1996–1997 (● – 0–1 cm, ○ – 1–10 cm). The shaded areas mark the flooded period

during the aquatic phase. Highest potential activities, however, were observed during the transition periods. High DEA values were accompanied by higher counts of nitrate-reducing bacteria (Fig. 14.6b) and also by high NO_3 concentrations as shown in Fig. 14.4b. The results indicate that denitrification plays a minor role during the terrestrial phase when it is limited by nitrate availability.

14.5 Nitrogen Balance of the Floodplain Forest

N gains via symbiotic N_2 fixation are important for the legumes themselves and also for the entire várzea forest. Disregarding other N sinks such as leaching and denitrification, there is not enough available nitrogen in the várzea soil for the annual requirement of the forest. Usually, rainwater and river water are important sources of nutrients for floodplains. In the várzea the N input by rainwater is rather low compared with the input by river water during the inundation period (Kern and Darwich 1997). The major pathway for N, however, is the várzea forest itself with high potential of N_2 fixation by legume trees. It could be shown in the case of the legume tree *Albizia multiflora* that despite leaching effects, there is an important fertilising effect.

Combining %Ndfa values with results from stand structure analyses, the average percentage of plant nitrogen derived from the atmosphere for the várzea forest was calculated to be between 4% and 5% (Kreibich and Kern 2004). Since the net biomass production of the várzea forest requires on average 322.7 kg N ha^{-1} year^{-1} according to Furch (1999), the nitrogen gain via nodulated legumes can be estimated to range between 12.9 and 16.1 kg N ha^{-1} year^{-1} (Table 14.6). Non-symbiotic N_2 fixation in the surface soil layer was 4.1 kg N ha^{-1} year^{-1} (Kreibich 2002). Since not all nodulated legume species are included in the estimate, and non-symbiotic N_2 fixation in deeper soil layers was neglected as was associative N_2 fixation, these are minimum values and actual N gain via N_2 fixation should be higher in the study area. It may be concluded that the gaseous N turnover plays

Table 14.6 N input and output fluxes to and from the várzea forest under study, measured or estimated as described in this chapter. Percentages of the input and output fractions are calculated for each pathway

N input to the forest	(kg N ha^{-1} $year^{-1}$)	(%)
Symbiotic N_2 fixation	12.9–16.1	48–54
Non-symbiotic N_2 fixation	4.1	12–17
Dry and wet deposition	2.6	8–11
Exchange with the river	4.4–10.5	18–32
Total N input	24.0–33.3	
N output from the forest		
Denitrification	12.5	56–63
Leaching	1.2–3.8	6–17
Exchange with the river	6.0	27–30
Total N output	19.7–22.3	

an important role in the forest area studied, covering 60–71% of all the N input paths and 56–63% of all the N output paths that have been calculated in this study. The high abundance of N_2 fixing legumes provides the main source for N, even surpassing the N gain via the river. This means that external paths of N input in the várzea forest are more responsible for the N availability than the effective N pool of the soil.

Denitrification with a mean rate of 12.5 kg N ha^{-1} $year^{-1}$ is the main pathway for N loss from the várzea soil, confirming results from low elevational ranges (Kern and Darwich 1997). On high elevational ranges within the várzea forest, however, N losses by denitrification seem to be counteracted completely by symbiotic N_2 fixation. Since total N input was calculated to be at least 24.0 kg N ha^{-1} $year^{-1}$, and maximum total N output to be 22.3 kg N ha^{-1} $year^{-1}$, a surplus of N can be assumed in the study area. By retention of N within the forest area of the várzea, N may accumulate within a pool, which becomes rich enough to enable high biomass increase and a succession of the mid-stage forest. The high biomass production of 322.7 kg N ha^{-1} $year^{-1}$ is far above the amount of nitrogen, which was calculated as input in this balance. Therefore internal N cycling is crucial to let this ecosystem work sustainably.

The nutrient balance of a tropical forest determines whether it can be utilised on a sustainable basis or not (Cole 1995; Whitmore 1998). There is a considerable N input via N_2 fixation and the flooding water, which suggests an open N cycle of the forest. According to the definition of Baillie (1989), closed nutrient cycles are defined as those where the ecosystem is sustained entirely by atmospheric deposition and internal cycling of nutrients, whereas in open nutrient cycles other sources such as N_2 fixation also exist. In the várzea forest, the amount of N stored in the biomass (1,479 kg N ha^{-1}; Furch 1997) is about 53 times the annual N input (24.0–33.3 kg N ha^{-1} $year^{-1}$). In terra firme forests this ratio is about 500 (Brouwer 1996). This means in terms of time that the floodplain forest is functioning more sustainably than upland forests.

14.6 Conclusions

Since N_2 fixation exceeded the N loss by denitrification, N_2 fixation plays a considerable role for the floodplain forest of the Amazon. In contrast to the non-symbiotic N_2 fixation, which is mostly restricted to the terrestrial period, there is whole-year N_2 fixation in the rhizosphere of nodulated legume trees. For one hydrological cycle, the N input by N_2 fixation within the forest was calculated to 17–20 kg N ha^{-1} $year^{-1}$. This natural fertilising effect indicates a sustainable carrying capacity, possibly to be used from an agronomic point of view. Looking at the entire rainforest of the Amazon region, sustainable management is urgently needed because the fragile upland forests have already been strongly affected. During recent decades the population of the Amazon region has increased rapidly and with it the pressure on the forest, bringing massive deforestation. Therefore landuse and agroforestry should be minimized or stopped in those forest regions with a low sustainable carrying capacity. One alternative could be to use sustainably the lowland forest of the várzea. It is comparatively small, but rich in nutrients. Limitation of plant growth by the available nitrogen may be compensated by N_2 fixation. Despite the difficulties due to periodical flooding, the cultivation of legumes and mixed-species systems may improve soil fertility and may transfer fertilising effects to associated crops. Such extensive forms of agro-forestry combined with the enhanced use of N_2-fixing plants in agro-forestry systems may be one appropriate way for sustainable development in the central Amazon region.

Chapter 15
Genetic Variability, Divergence and Speciation in Trees of Periodically Flooded Forests of the Amazon: A Case Study of *Himatanthus sucuuba* (Spruce) Woodson

Cristiane S. Ferreira, Antonio V.O. Figueira, Rogério Gribel, Florian Wittmann, and Maria T.F. Piedade

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Abstract Contrary to the theory that geographic isolation is the main trigger for speciation, recent studies emphasize the continuous adaptation to different habitats as the driving force initiating diversification. In this way, adaptive divergence in response to contrasting selective pressures of populations of the same species in

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geographically or ecologically continuous environments may occur if long-lasting barriers are induced by biotic or abiotic events. Plants of the Amazon floodplains withstand annual periods of flooding which can last seven months. To verify if the regularity of the "flood pulse" of the Amazon River can induce speciation, we investigated populations of Himatanthus sucuuba (Apocynaceae) colonizing whitewater floodplains (várzea) and non-flooded uplands (terra-firme) in the region. In independent experiments, we simulated flooding conditions, to evaluate the germination and growth of seedlings from both environments. The two populations showed significant differences for most parameters evaluated. Thus, flooding is apparently a feature strong enough to promote phenotypic differentiation among várzea and terra firme populations. Indeed, molecular analysis showed genetic difference between populations, revealing that different ecological pressures may promote adaptive changes in Amazonian plants to insure establishment in different environments.

15.1 Introduction

Contrary to the theory that geographic isolation is the main trigger for speciation, recent studies emphasize the continuous adaptation to different habitats as driving force initiating diversification (Smith et al. 2001; Rieseberg and Wendel 2004). In this case, the separation of individuals of the same species in geographically or ecologically continuous environments may occur if barriers are induced by biotic or abiotic events capable to initialize an adaptive divergence. In combination with the genetic attribute of a population, intensity and duration of this event may cause that adaptive divergence leads to speciation.

The ability of plants to make morphological or physiological adjustments in response to environmental cues allows them to survive and reproduce under a wide range of conditions (Benz et al. 2007). However, due to the variety of possible phenotypic responses of the same species colonizing different ecosystems, contrasting adaptive strategies may lead to a geographic isolation of morphotypes and to evolutionary divergence (Benz et al. 2007; Ferreira et al. 2007).

In Amazonia, the taxonomic identification of species by means of usual morpho-anatomic species descriptions is often difficult due to the complexity of ecosystems, which often lead to the occurrence of ecotypes of different forms, habits and physiological behaviors (Souza 2006). The existence of cryptic species (two or more distinct species classified as a singular species) is a challenge for taxonomists since several hundreds of years. As speciation is not always accompanied by visible morphological differences, it is likely that the real number of species is higher than the number of species described by classic taxonomists (Bickford et al. 2007). Therefore, the application of molecular techniques in taxonomic and systematic studies certainly will modify the existing species lists and eventually increase species diversity at regional scales.

15.2 Flood Tolerance and Speciation in Flooded Forests

No one has formulated a hypothesis about the consequences of ecological instability on várzea forests to the phylogeography of trees. The recurrent perturbation episodes that this type of environment is exposed to, in the scale of a few million years, probably result in events of extinction and/or population bottlenecks, with the consequent reduction in the genetic diversity of the populations in comparison to the populations that occur in the more stable environments of the terra firme forests.

Paleoclimatic and paleobotanic evidences apparently support that the colonization of the floodplains has occurred from the terra firme species that have invaded the flooded areas during recent paleoclimatic events (Haffer and Prance 2001). In this case, the degree of adaptation would be dependent on the extent of time that the colonization of these environments has occurred, as well as on the adaptability potential of the different species (Kubitzki 1989c; Parolin 2001a). Therefore, species richness of the floodplains would result from parallel immigration of pre-adapted species and subsequent specialization and differentiation (Parolin 2003). Irrespective of the differing abiotic conditioners that predominates in terra firme and várzea forests, studies in central Amazonia have demonstrated that their flora show a similarity of about 30% of coincidences at the species level (Wittmann et al. 2006a), and which are regarded as species that possess large phenotypic amplitude.

Tolerance to environmental stresses is triggered by a pool of genes that acts in concert in the plant, modulating species metabolism (Way et al. 2005; Zhang et al. 2005; Pigliucci and Kolodynska 2002). Their efficiency can therefore result in individuals with larger or smaller tolerance to the environmental stresses to which they are exposed. In this case, a question that immediately emerges is if the populations of the same species that inhabit the terra firme and the várzea forests would have the same degree of tolerance to flooding as the ones that inhabit the flooded areas or if these two environments could act as speciation sites.

Questions of this nature emerge because the várzea forest can be regarded as an environment capable of promoting recurrent adaptive changes in plants, which impose at first metabolic adjustments that, in the last instance, can induce modifications in the anatomy and even in the morphology to insure survival and the species perennization in the environment. In this case, the flood pulse could be considered a feature strong enough to favor the action of natural selection in these environments. Indeed, studies of contiguous habitats in tropical forests in Australia (Smith et al. 2001) have shown that speciation can be prompted by an ecological gradient, independent of the presence of gene flux.

In addition to be subjected to the selective pressures imposed by the flood pulse, which propitiate a clear species zonation along the flooding gradient, várzea forests can be separated from the closest terra firme forests by rivers of great dimensions, like the Solimões/Amazon river. 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 fact, it is not difficult to suppose that these factors operating in concert can serve as agents of speciation in the floodplains. It is not possible to establish a pattern, and to state that this process occurs to all species that have populations in both ecosystems. In fact, studying the phylogeography of frogs and small mammals, Gascon et al. (2000) suppose that a putative riverine barrier (the Juruá River) does not relate to present-day patterns of community similarity and species richness. On the other hand, other studies have provided support for the hypothesis that large lowland Amazonian rivers have functioned as significant impediments to gene flow among populations of neotropical species (e.g. Hall and Harvey 2002). It is probable that the postulated role of rivers as major drivers of Amazonian diversification acts in places where the influence of these factors is more strongly experienced (for instance in the low várzea).

For widely distributed tree species such as *Himatanthus sucuuba* and *Calophyllum brasiliensis* which are able to colonize both the várzea and terra firme habitats, the conditions for divergence and speciation are expected to occur at the geographical and ecological boarders of the species distribution, from subpopulations that are locally adapted. According to Price et al. (2003), adaptation of an individual to a new habitat is related to the appearance of multiple traits, plastic or not, which will form more complex features involved in the adaptive response. These responses, once they are established in the phenotype, can induce selection on the morphology and physiology of those species, and act as a potent evolutionary force in new directions.

Following this line of reasoning, it is possible to delineate what direction the evolutionary process will take. Thus, if one supposes that the traits that would lead to the adaptation of a species to flooding would appear in the high várzea habitats, the speciation process would be evident in the low várzea. The high várzea, in this case, can be seen as a pre-selective environment, which would require that the plant has adaptations to prevail under conditions of excess water in the soil. Only after these conditions are met the species would be able to radiate, depending on their degree of adaptability. This fact would result in migration to the lower portions of the várzea, where they would be subjected to speciation, as evidenced by the high endemism observed in this type of habitat. On the other hand, those species that do not tolerate prolonged flooding conditions, would not be able to invade the lower várzea and would be restricted to the higher várzea areas, where the duration and intensity of the flood pulse are smaller.

15.3 *Himatanthus sucuuba*: A Case Study from Central Amazonia

Plants subjected to periodical inundations generally develop specific adaptations to cope with periods of reduced oxygen supply during all stages of life. Thus, it is reasonable to expect that species highly adapted to inundation are restricted to the periodically flooded várzea forests, and would not occur in non-flooded terra firme forests. The habitat specialization was reported by Fine et al. (2004) in a study of seedlings of 20 Amazon species, which were either specialists of nutrient-rich clay soils or nutrient-poor white sand soils. Seedlings of species that were from forests in clay soils invested in growth and less in herbivore defenses. Clay specialists grew significantly faster in both soil types when protected from herbivores. However, when planted in white-sand habitats they have not invested enough in defense mechanisms and were subjected to intense herbivory pressure which severely restricted establishment and growth they were outperformed by the white sand specialists in this type of habitat. In this particular case there was a clear trade-off between allocation to growth and to antiherbivore defense. Maintenance of habitat specialization was the result of an interaction between herbivore pressure with soil type.

A similar reasoning could apply for flooded forest. This could be, for instance due to the trade-off between high investment in anaerobic metabolism at the expenses of growth, which would limit their potential to successfully compete for light in the shaded understorey of terra firme forests. However, there exist several Amazonian tree species which occur in both ecosystems (e.g. *Himatanthus sucuuba*). If the wide distribution pattern in these species is reflected by a large phenotypical plasticity that propitiates temporarily tolerance to flood stress, studies focusing on potentially stressful conditions become increasingly important for the understanding of tolerance, adaptation and speciation.

On the other hand, even taxonomically classified as the same species, the terra firme population is maybe non-tolerant or shows different adaptive responses to inundation when compared to the floodplain population. In this case, distinct adaptive behavior between populations suggests a certain degree of genetic separation.

15.3.1 Phytogeographical, Botanical, and Ecological Characteristics of H. sucuuba

The genus *Himatanthus* (Apocynaceae) consists of 13 South-American species that all occur between 10ºN and the Tropic of Capricorn, with predominance in the Amazon basin (Plumel 1991). The occurrence of *H. sucuuba* (Fig. 15.1) was described in flooded and non-flooded forests of the Amazon basin within Venezuela, the Guyanas, Bolivia, Peru, and Brazil, where the species was found in the States of Pará, Amazonas, Mato Grosso, Rondônia, and Acre (Plumel 1991, INPA herbarium). Its occurrence is mostly in low-várzea forests, where the populations undergo mean inundated periods of approximately 5 months per year, and in non-flooded terra firme forests along the margins of the Solimões/Amazon River.

15.3.2 Divergence in Germination and Establishment

Germination behaviour and establishment between populations of *H. sucuuba* originating from seeds from (a) várzea and (b) terra firme were strikingly different. Seeds of the population (a) germinated and established when experimentally inundated (Table 15.1). Though seeds of the population (b) protruded radicles in the same experimental setting, the seeds subsequently suffered necrosis leading to the death of the embryo. In no case, seeds originating from population (b) developed seedlings when inundated (Ferreira et al. 2007).

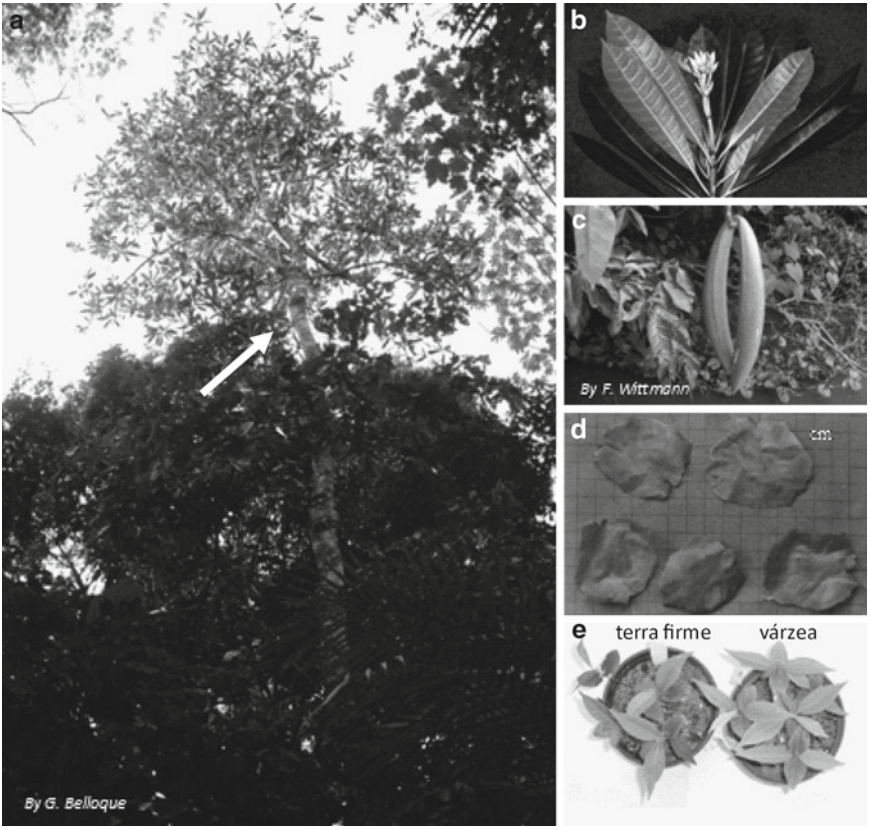

Fig. 15.1 An emerging *Himatanthus sucuuba* tree in the low-várzea forest (**a**). Details of the branch with terminal inflorescences (**b**); fruit (**c**); ellipsoidal seeds, covered by a well-developed circular wing membrane (**d**); seedlings from the terra firme and várzea populations (**e**)

Table 15.1 Germination (%) and seedling emergence (%) in *H. sucuuba* seeds from várzea and terra firme populations. Seeds were placed in trays and subjected to two hydric conditions: non-flooded (irrigated, sand + sawdust substrate) and flooded (seeds submerged in a water column of 5 cm). Data represent mean values ± Standard deviation (Adapted from Ferreira et al. 2007)

	Germination (%)		Seedlings (%)	
Origin	Non-flooded (sand + sawdust)	Flooded (submerged in water)	Non-flooded (sand + sawdust)	Flooded (submerged in water)
Várzea	94 (±2.6) A	98 (±1.7) A	94 (±1.7) A	84 (±2.9) A
Terra firme	91 (±0.8) A	64 (±1.0) B	91 (±2.1) A	0 B

Numbers followed by equal characters within the same column are non-significant (Tukey 5%), n = 100

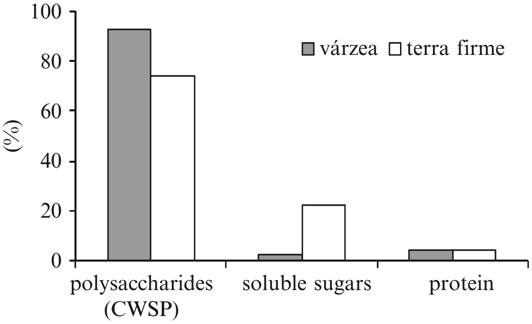

Fig. 15.2 Endosperm constituents in seeds of *H. sucuuba*

Within Amazonian floodplain forests, fast germination and fast seedling development are especially important because trees must fix their roots on substrate during the restricted periods of low water levels, before inundation reaches the sites. This strategy is reflected by different chemical compounds found in analyses of the endosperms of the várzea and the terra firme populations (Fig. 15.2). In seeds originating from the várzea, more than 90% of the endosperm reserves are constituted of pure mannan (Ferreira 2006), a cell wall storage polysaccharide (CWSP) that is responsible for hardness and water impermeability of the seed, and whose mobilization occurs after germination, during plant establishment (Buckeridge et al. 2004). In seeds originating from the terra firme, polysaccharides amount to 74% of the endosperm reserves, and are constituted of galactomannan (Ferreira 2006), a CWSP that absorbs humidity and that functions as a provider of water and carbon for the embryo (Potomati and Buckeridge 2002). Approximately 22% of the endosperm reserves are soluble sugars (Fig. 15.2), which are mobilized during the process of germination. These results suggest that seeds originating from the várzea invest more in reserves that secure plant establishment, whereas seeds originating from the terra firme invest more in reserves that secure germination (Fig. 15.2).

During the periods of seedling establishment at the terrestrial phase, seedling biomass was two times higher in várzea seedlings (6.52 g) than in terra firme seedlings (3.02 g). Besides, biomass accumulation in the different parts of the seedlings was distinct between both the populations. The várzea seedlings accumulated more biomass in the roots (36%) and in stalks (39%), but less in leaves (25%), whereas the terra firme seedlings accumulated more biomass in the leaves (44%) and the stems (30%), and less in roots, which accounted for only 26% of total biomass (Ferreira 2006; Ferreira et al. 2007). Sucrose was the main sugar reserve in the roots of both populations (Ferreira 2006), but with significantly higher amounts in the roots of the várzea population (167.3 $mg.g^{-1}$ dry matter) than in the terra firme population (101.3 $mg.g^{-1}$ dry matter). This result can be interpreted as effective adaptation to the periodical inundations, because seedling survival depends on root activity, which in turn requires a permanent minimum quantity of energy (Lobo and Joly 1998). During the terrestrial phase, seedlings from *H. sucuuba* originating from the várzea accumulate reserves in their roots that guarantee metabolism in subsequent inundations.

15.3.3 Morphological, Anatomical, and Physiological Responses to Flooding

In the two investigated populations, várzea and terra firme, complete submersion of the seedlings during a period of 30 days caused leaf abscission and induced the formation of aerenchymatic tissue in the roots. The seedlings entered a physiological dormancy, stopped height growth and reduced the use of carbohydrate reserves (Ferreira 2002; 2006; Ferreira et al. 2007). The analysis of the anaerobic metabolism enzyme alcohol dehydrogenase (ADH) indicated that *H. sucuuba* divert the metabolic route to the formation of ethanol as final product when under anaerobiosis (Ferreira et al. 2006). This enzyme showed elevated activity after initialization of experimental inundation (Fig. 15.3a). One consequence of anaerobic metabolism is the formation of highly toxic compounds that may lead to plant death when accumulated (Crawford 1992; Kozlowski 1997). In this case, tolerance to flooding is directly linked to the capacity of the development of mechanisms which promote detoxication thus securing plant survival (Crawford 1978; Harborne 1988; Ferreira et al. 2006). This ability varies between the populations of *H. sucuuba*, indicating one tolerant (várzea) and one non-tolerant (terra firme) population to anaerobic site conditions.

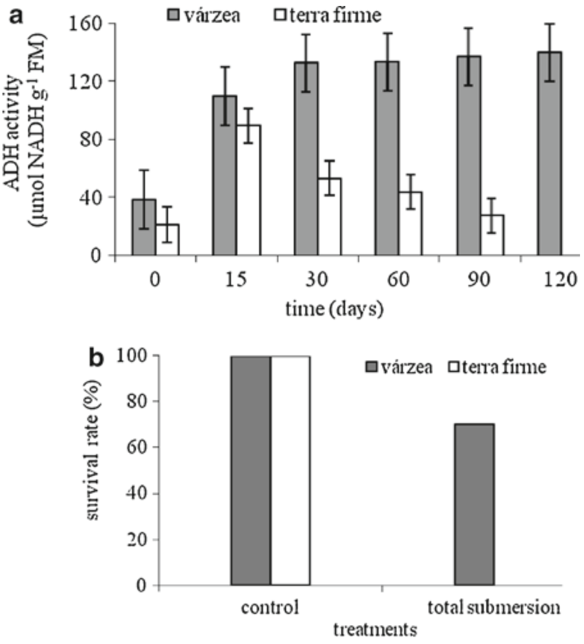

Fig. 15.3 ADH enzyme activity in seedling populations of *H. sucuuba* originating from the várzea and the terra firme, after 120 days of experimental submersion (**a**); Survival rate of the species after the experiment (**b**). No seedling originating from the terra firme population survived 120 days of total submergence (Ferreira 2002)

No seedling originating from the terra firme population survived the experiment of 120 days of complete seedling submersion. First, necrosis affected the roots afterwards extending to the whole plant, leading to death (Fig. 15.3b). Survival rates in seedlings originating from the várzea amounted to 70% (Fig. 15.3b), all seedlings being characterized by elevated ADH activity at the end of the experiment (Fig. 15.3a).

15.3.4 Genetic Structure

The analysis of chloroplast DNA via micro-satellites of simple sequence (loci *ccmp2*, *ccmp3* e *ccmp7*, according to Weising and Gardner 1999) did not show polymorphisms between the várzea and terra firme populations in the visualized bands.

Because it deals with conserved DNA, the analysis of cpDNA allows us to conclude that species with pioneer traits and rapid dispersal as *H. sucuuba,* may be favored in colonizing the várzea. The founding effects, important in recent colonization processes may result in a reduced number of motherly lineages in the population settled in the particular habitat. As a consequence a low diversity, particularly of the genome's organelles – with motherly heritage – would be expected for the várzea populations. A virtual lack of genetic structure in the genome of the chloroplast has been recently registered for the long living pioneer species *Ceiba pentandra* from Africa and the Neo-tropics (Dick et al. 2007), including four populations from the Amazon várzea.

On the other hand the analyses of sequences from regions of the gene nuclear ribosomal (rDNA), including ITS-1 and ITS-2 (*Internal Transcribed Spacer*), and those of the gene 5.8S revealed divergence of the genetic structure between the várzea and the neighboring terra firme populations. Sequenced fragments of the 687 and 754 pb were amplified for the várzea and terra firme populations, respectively (Table 15.2). The confirmation of the nucleotide sequence identity of the cloned fragments was done by comparing them with ITS1 and ITS2 sequences of the rDNA of other species, including individuals of the Apocynaceae family, available at the data bank GenBank (http://www.ncbi.nih.gov). The same analyses were performed with individuals of *H. sucuuba* colonizing sites in the várzea and terra firme, about 1,400 km far from Manaus, in the County of Benjamin Constant, upper Solimões River, in order to verify if the same pattern of divergence was constant.

Table 15.2 Size of the fragments amplified via PCR using the *primers* ITS-18S and ITS-4, for populations from terra firme (TF) and várzea (VZ) of two geographic regions within the Amazon Basin (Manaus and Benjamin Constant, 1,400 km distant from each other)

Location	Size of the fragment (in pb)
TF – Manaus	754
VZ – Manaus	687
TF – Benjamin Constant	690
VZ – Benjamin Constant	690

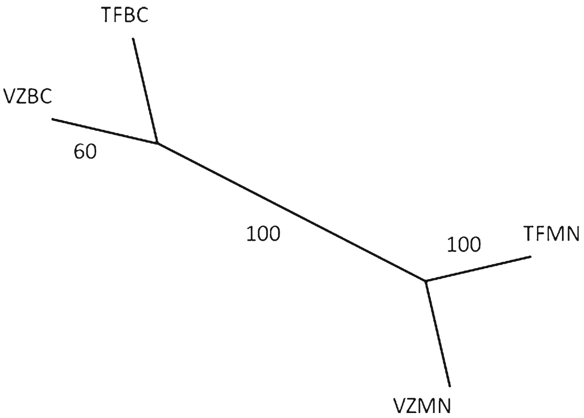

Fig. 15.4 Phylogram resulting from the alignment of the sequences of ITS1-58.S–ITS2 of the nuclear rDNA from individuals of *H. sucuuba* populations at the várzea and terra firme in Benjamin Constant and Manaus regions. VZBC – várzea of Benjamin Constant; TFBC – terra firme of Benjamin Constant; VZMN – várzea of Manaus; TFMN – terra firme of Manaus

The phylogenetic analyses were conducted using the software PAUP 4.0b10 (Swofford 1998), which permitted the construction of a phylogram by means of the "Neighbor-joining" method (Saitou and Nei 1987). A consensual tree resulting of these analyses (Fig. 15.4) had the support of its clades evaluated by *bootstrap* tests with 1,000 replications (Felsenstein 1995), allowing to point out the clear disjointing (*bootstrap* 100%) between the *H. sucuuba* populations established at the várzea and terra firme in the Central Amazon. The results corroborate the proposition of Ferreira et al. (2007), that the extreme environmental constraints imposed by flooding in the Amazonian várzea may lead to speciation in tree species.

The analyses revealed that although both the populations of várzea and terra firme are diverging (*bootstrap* 60% between the VZ and TF populations in Benjamin Constant; *bootstrap* 100% between the VZ and TF populations in Manaus), they aggregate consistently between them (*bootstrap* 100%), when the geographic regions sampled are related, pointing out a larger local similarity in comparison to the similarity verified at the latitudinal gradient (Fig. 15.4).

15.4 Conclusions

In the comparison of species populations of *H. sucuuba* between várzea and terra firme in the regions of Manaus and Benjamin Constant (near the frontier Brazil-Colombia), Ferreira et al. (2006) confirmed that populations of *H. sucuuba* inhabiting the várzea originate from adjacent non-flooded terra firme populations. The results of the ITS sequences in the different populations of várzea and terra firme show that the differences between these populations were consistent in each region, whereas no relation could be detected between both geographic regions (*bootstrap* 100%). We therefore suggest that the colonization of floodplains by this species in each of the geographic regions depends on the existent genetic pool of the populations in adjacent terra firme forests.

The results available so far suggest that the genetic structure of Amazonian tree populations – at least of the few analysed species – varies in function of life history and evolutionary history of the species. The kind of molecular marker used seems to influence the divergence patterns found, turning difficult the comparison among species studied with different markers. For example, for virtually all tropical trees studied so far using isoenzymes, the genetic diversity within populations is significantly higher than that found among populations (Buckley et al. 1988; Hamrick and Loveless 1989; Loveless 1992). These findings contrast with those found for *H. sucuuba* populations using ITSs markers.

In *Vouacapoua americana* (Caesalpiniaceae), a primary forest tree which is tolerant to shade, entomophilous and with limited seed dispersion, ten different chloroplastid DNA haplotypes were found based on PCR-RFLP analysis, just in the French Guianan territory (Dutech et al. 2000). A high genetic differentiation of the chloroplast genome was observed among studied populations that revealed areas of some thousand hectares with just one haplotype. This pattern suggests that extinction and colonization processes shaped the distribution of the genetic diversity in contemporary populations of *V. americana*, probably due to climate variation during the Pleistocene and Holocene. In contrast, in *Symphonia globulifera* (Clusiaceae), a tropical tree with African and neotropical distribution, dispersed by a range of vertebrates (ruminants, monkeys, bats, large birds), no nucleotidic variation in ITS was found in collected samples of a large region covering French Guiana, Brazilian Amazonia, eastern Ecuador and Bolivia (Dick et al. 2003). The populations of the west Andes and Central America, however, displayed considerable phylogeographic structure when analysed with the same markers, suggesting that the more instable climatic history and heterogeneous topography of Mesoamerica, in comparison with Amazonia, caused greater isolation and genetic differentiation in tree populations. Greater genetic differentiation in populations localized in regions of high topographical complexity was also found for Amazonian and Mesoamerican populations of mahogany (*Swietenia macrophylla*, Meliaceae) using nuclear genome microsatellites (Lemes et al. 2003; Novick et al. 2003).

Amazonian várzea forests are characterized by a high number of endemic tree species (approximately 40%). From these endemic tree species, the majority (approximately 68%) occur at low topographic positions along the flooding gradient, where inundation lasts for periods > 6 months year^{-1} (low várzea *sensu* Wittmann et al. 2002b). Together with generally low floristic similarities between low-várzea and terra firme forests across the Amazon basin (<10%), the concentration of endemic tree species in highly flooded low-várzea forests have led to the development of the Species Colonization Concept (SCC) in várzea forests (Wittmann et al. 2010).

The SCC argues that the continuous immigration of terra firme species to the várzea, the eventual return of várzea species to the terra firme, and the degree of speciation within the várzea are triggered by extreme environmental events, like the climatic changes during the Pleistocene (Haffer and Prance 2001). Once established at low topographic positions within the várzea and adapted to extreme flooding, low-várzea species occupy ecological niches where the annual flood-pulse (Junk et al. 1989) controls highly specific mechanisms of dispersal and establishment. The hydrological connectivity favors genetic fluxes between low-várzea species (Pires 1984; Kubitzki 1989c), thus maintaining high levels of endemism within the várzea flora. However, the genetic fluxes between plants depend strongly on their reproductive biology and thus involve pollinators and seed dispersers and their movements and efficiencies. In this context, detailed studies about *H. sucuuba* considering these aspects are fundamental.

The genetic diversity of *H. sucuuba* might be of substantial importance for species survival under future climate change, because specific adaptations to a given environment imply high vulnerability to extreme environmental changes. If extreme water level changes – as they were predicted in climatic models of the Intergovernmental Panel on Climate Change-IPCC-UNO) affect the large rivers of the Amazon basin, the stress on the várzea vegetation would increase, probably changing species distribution and diversity patterns. Intense research about the floodplain vegetation is necessary to better describe the actual stage of species diversity, the presence of cryptic species, and for a better understanding of the mechanisms responsible for the speciation processes.

Chapter 16
The Importance of Amazonian Floodplain Forests for Animal Biodiversity: Beetles in Canopies of Floodplain and Upland Forests

Joachim Adis†, Terry L. Erwin, Leandro D. Battirola, and Suzana M. Ketelhut

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16.1 Introduction

Thirty-one 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.

16.2 Material and Validity of Data

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

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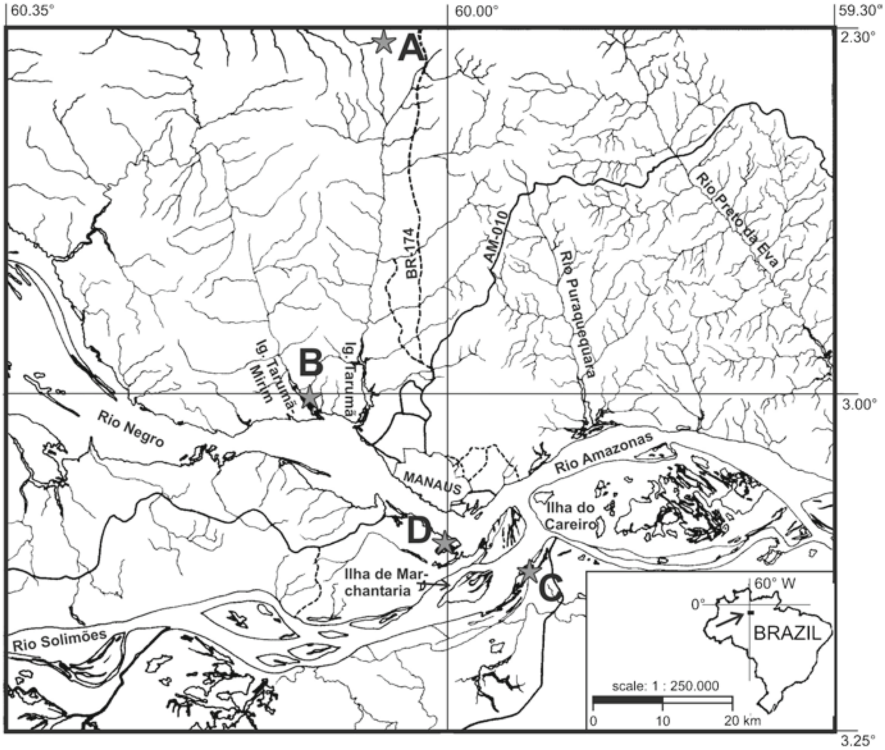

Fig. 16.1 Sampling sites at Manaus. (**a**) primary upland forest (terra firme; km 20 at ZF-2: 02°34′S, 60°06′W); (**b**) Blackwater inundation forest (igapó; Rio Taruma Mirim: 03°02′S, 60°17′W); (**c**) whitewater inundation forest (várzea; Ilha de Curarí: 03°15′, 59°49′W)); (**d**) mixedwater inundation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

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

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

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

	Forests			
Parameters	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
Eveness (E)	0.953	0.941	0.931	0.925

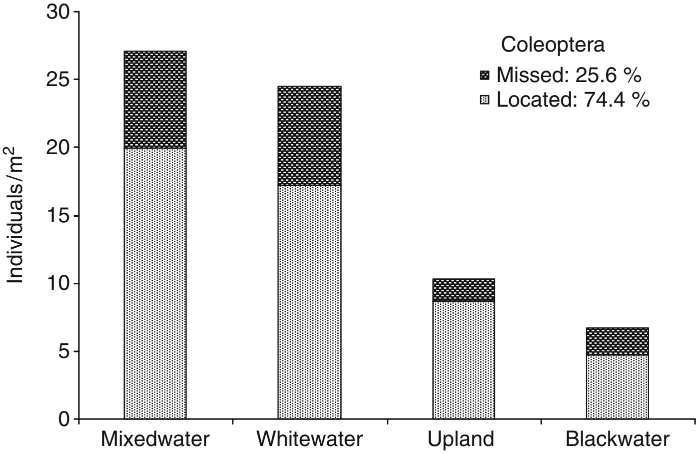

Fig. 16.2 Abundances of Coleoptera (ind./m^2) evaluated by Erwin (1983) and in this study (*lower bars*) from the canopy of four forest types in Central Amazonia

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; Cylindrorhinae = Cyclominae; Erirhininae = Erirhinidae; Hylobinae = Molytinae: Hylobiini; Magdalinae = Mesoptiliinae; Myrmecinae = Otidocephalini; Prionomerinae = Molytinae: Camarotini and Piazorhini; Rhynchitinae = Attelabidae: Rhynchitinae; Rhynchophorinae = Dryophthoridae; Zygopinae = Conoderinae; see Alonso-Zarazaga 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 to Simberloff, and patchiness (Chi-square test) the Biodiversity Professional Programme (version 2) of Gage and McAleece (1979) was used. Magurran (1988) was followed to calculate diversity indices of Shannon (H) and Simpson (D) with log base e, as well as the Berger-Parker dominance index and eveness.

16.3 Results

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

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

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

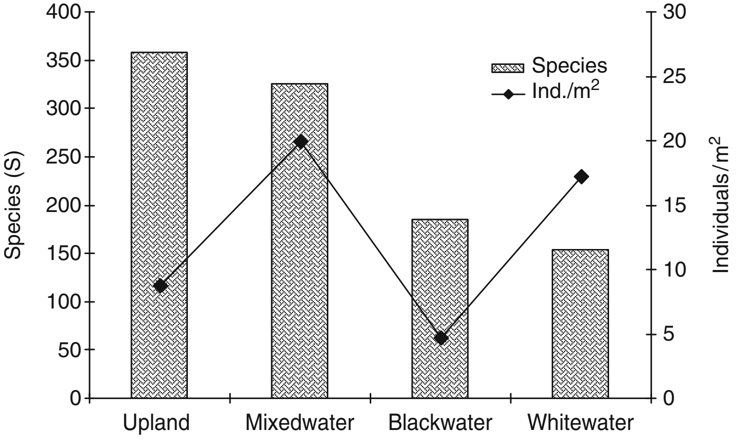

Fig. 16.3 Total number of species (S) and abundances (ind./m²) of Coleoptera evaluated from the canopy of four forest types in Central Amazonia

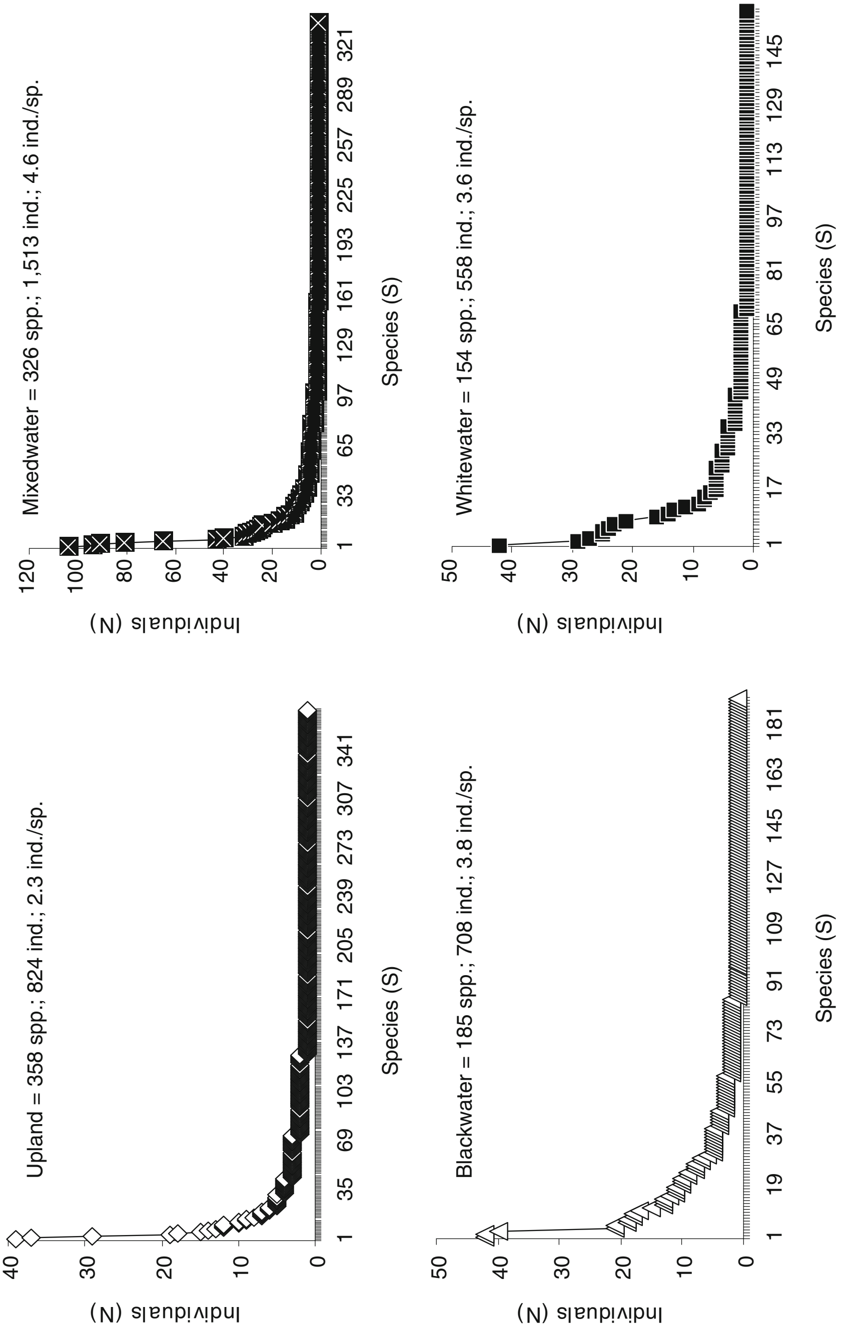

Fig. 16.4 Rank-abundance curves of Coleoptera specimens and species (N/S) evaluated from the canopy of four forest types in Central Amazonia

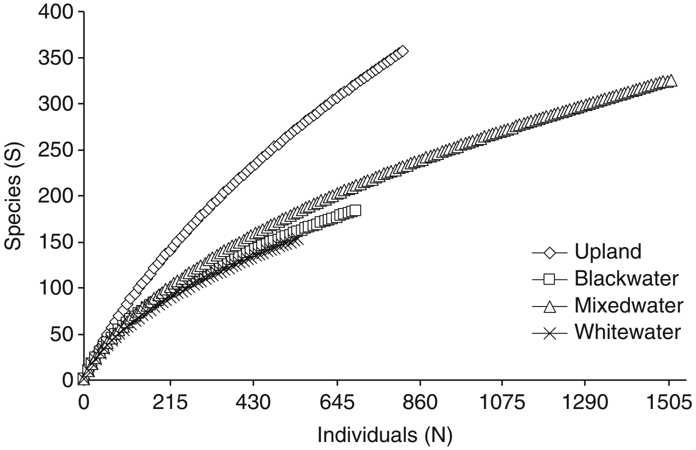

Fig. 16.5 Rarefaction curves of Coleoptera species and specimens (S/N) evaluated from the canopy of four forest types in Central Amazonia

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

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

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

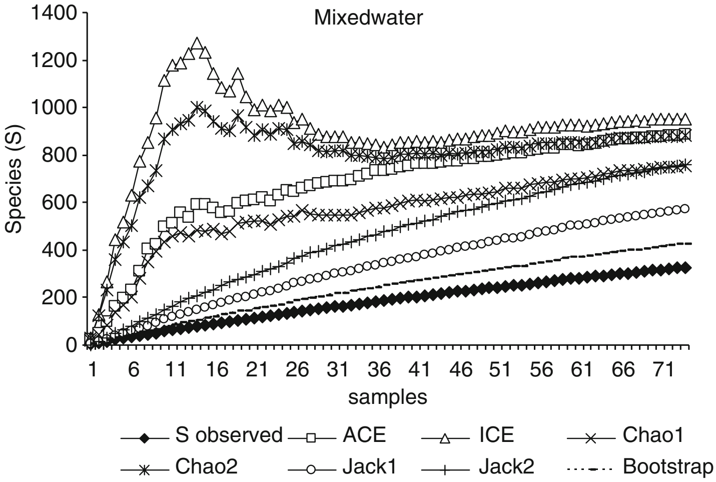

Fig. 16.6 Observed and calculated species richness for the Coleoptera evaluated from the canopy of a mixedwater inundation forest in Central Amazonia

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

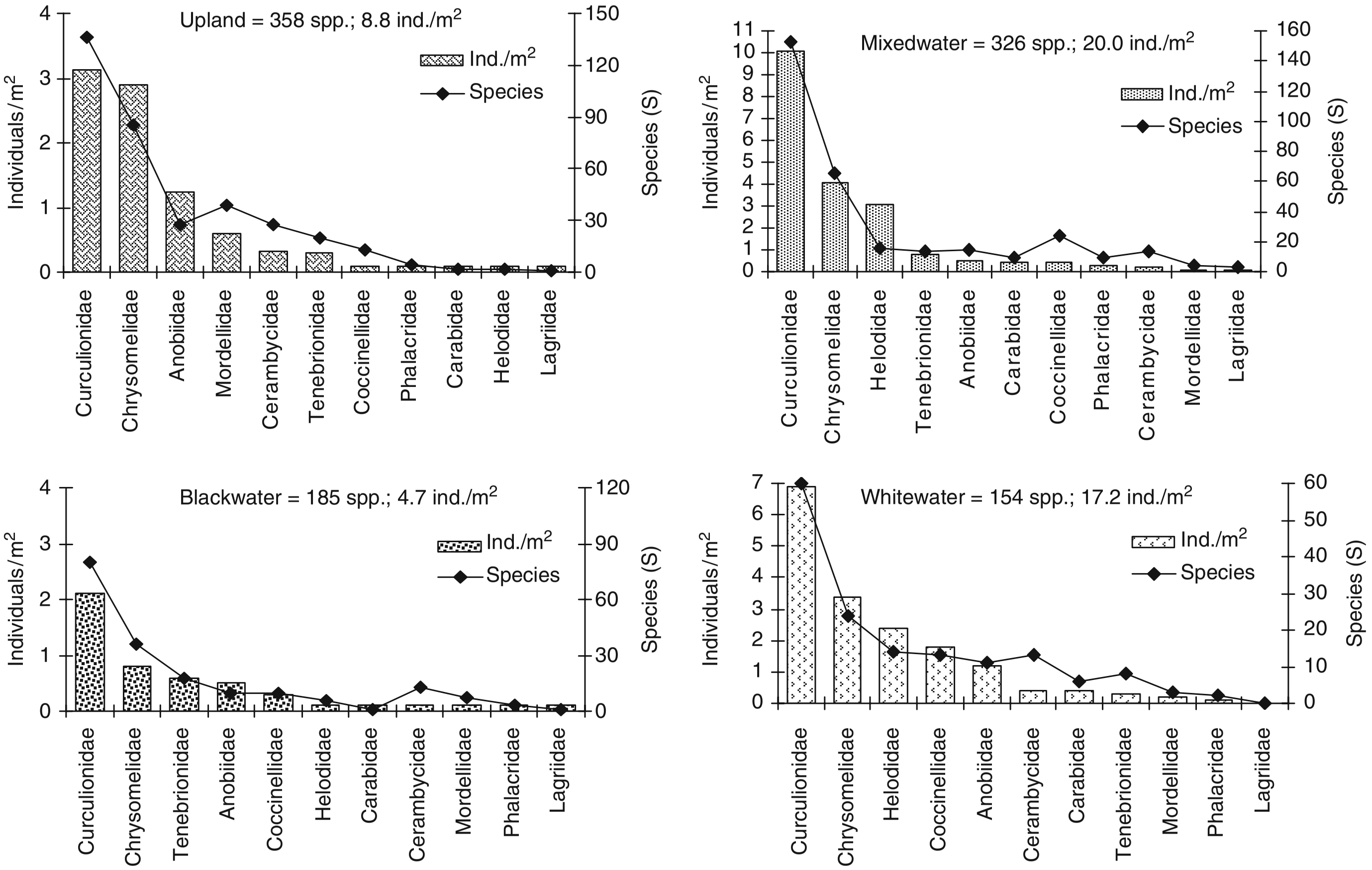

Fig. 16.7 Abundances (ind./m^2) and number of species (S) of Coleoptera families evaluated from the canopy of four forest types in Central Amazonia

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. (%)			
Herbivores (%)[a]	748	270 (92.5) (36.1)	105 (73.9) (14.0)	188 (72.7) (25.1)	73 (63.5) (9.8)	635 (84.8)	101 (13.5)	9 (1.2)	4 (0.5)
Cerambycidae	63	26 (83.9)	12 (70.6)	10 (55.6)	11 (78.6)	59 (93.7)	3 (4.7)	1 (1.6)	–
Lagriidae	5	1 (100.0)	1 (100.0)	3 (100.0)	–	5 (100.0)	–	–	–
Curculionidae	374	120 (88.9)	58 (71.6)	112 (73.2)	36 (61.0)	325 (86.7)	48 (12.8)	2 (0.5)	–
– Anthonominae	14	7 (87.5)	–	3 (60.0)	2 (100.0)	12 (85.7)	2 (14.3)	–	–
– Apioninae	124	36 (92.3)	25 (96.2)	47 (82.5)	6 (46.2)	115 (92.0)	10 (8.0)	–	–
– Attelabinae	3	2 (66.7)	–	–	–	2 (66.7)	1 (33.3)	–	–
– Baridinae	15	2 (100.0)	2 (66.7)	8 (61.5)	2 (66.7)	14 (93.3)	1 (6.7)	–	–
– Broadnose families (Entiminae)	12	4 (50.0)	–	3 (75.0)	–	7 (58.3	5 (41.7)	–	–
– Ceutorhynchinae	2	–	–	1 (50.0)	–	1 (50.0)	1 (50.0)	–	–
– Cholinae	2	2 (100.0)	–	–	–	2 (100.0)	–	–	–
– Cossoninae	3	1 (50.0)	–	–	–	1 (33.3)	2 (66.7)	–	–
– Cryptorhynchinae	100	28 (87.5)	14 (70.0)	35 (79.5)	14 (77.8)	89 (89.0)	10 (10.0)	1 (1.0)	–
– Cylindrorhininae	1	–	–	1 (100.0)	–	1 (100.0)	–	–	–
– Erirhininae	5	2 (66.7)	–	–	1 (33.3)	3 (60.0)	2 (40.0)	–	–
– Hylobiinae	19	8 (100.0)	4 (66.7)	3 (50.0)	1 (25.0)	15 (78.9)	3 (15.8)	1 (5.3)	–
– Hyperinae	2	–	–	–	1 (100.0)	1 (50.00)	1 (50.0)	–	–
– Magdalinae	4	3 (100.0)	–	–	1 (100.0)	4 (100.0)	–	–	–
– Myrmecinae	13	6 (100.0)	2 (66.7)	2 (40.0)	–	10 (76.9)	3 (23.1)	–	–
– Prionomerinae	7	–	–	4 (80.0)	2 (66.7)	6 (85.7)	1 (14.3)	–	–
– Rhynchitinae	3	3 (100.0)	–	–	–	3 (100.0)	–	–	–
– Rhynchophorinae	1	1 (100.0)	–	–	–	1 (100.0)	–	–	–

(continued)

Table 16.2 (continued)

		Only UL	Only BW	Only MW	Only WV	Restricted, one forest	Shared, two forests	Shared, three forests	Shared, four forests
	Σ spp.	(%)^a				Σ spp. (%)			
		270 (92.5)	105 (73.9)	188 (72.7)	73 (63.5)				
Herbivores (%)^a	748	(36.1)	(14.0)	(25.1)	(9.8)	635 (84.8)	101 (13.5)	9 (1.2)	4 (0.5)
– ychiinae	2	–	–	–	–	0 (0.0)	2 (100.0)	–	–
– Zygopinae	38	14 (87.5)	4 (84.6)	4 (57.1)	6 (100.0)	35 (92.1)	3 (7.9)	–	–
– Nonidentifiable	4	1 (100.0)	–	1 (50.0)	–	3 (75.0)	1 (25.0)	–	–
Chrysomelidae	178	69 (81.2)	24 (66.7)	43 (66.2)	15 (60.0)	151 (84.8)	24 (13.5)	3 (1.7)	–
– Alticinae	73	21 (70.0)	12 (66.7)	21 (67.7)	6 (66.7)	60 (82.2)	11 (15.1)	2 (2.7)	–
– Cassidinae	3	2 (100.0)	–	–	1 (100.0)	3 (100.0)	–	–	
– Chlamysinae	5	2 (100.0)	–	1 (100.0)	2 (100.0)	5 (100.0)	–	–	–
– Chrysomelidae	4	–	1 (50.0)	1 (100.0)	1 (100.0)	3 (75.0)	1 (25.0)	–	–
– Cryptocephalinae	22	12 (92.3)	1 (100.0)	7 (87.5)	1 (50.0)	21 (95.5)	1 (4.5)	–	–
– Eumolpinae	61	31 (88.6)	9 (75.0)	8 (44.4)	3 (33.3)	51 (83.6)	9 (14.8)	1 (1.6)	–
– Galerucinae	5	–	–	3 (75.00)	–	3 (60.0)	2 (40.0)	–	–
– Hispinae	1	–	–	1 (100.0)	–	1 (100.0)	–	–	–
– Lamprosomatinae	4	1 (100.0)	1 (100.0)	1 (100.0)	1 (100.0)	4 (100.0)	–	–	–
Helodidae	29	2 (100.0)	6 (100.0)	7 (43.8)	5 (35.7)	20 (69.0)	9 (31.0)	–	–
Mordellidae	45	33 (84.6)	2 (28.6)	3 (75.0)	1 (33.3)	39 (86.7)	5 (11.1)	1 (2.2)	–
Anobiidae	42	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	12	1 (25.0)	1 (33.3)	5 (55.6)	–	7 (58.4)	4 (33.3)	1 (8.3)	–
Scavengers (= Saprophages)	48	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	48	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)	–	–	–	–

[a] Herbivores (%)

[b] Scavengers (= Saprophages)(%)

[c] Predators(%)

[d] Total(%)

UL = upland forest, BW = blackwater forest, MW = mixedwater forest, WW = whitewater forest

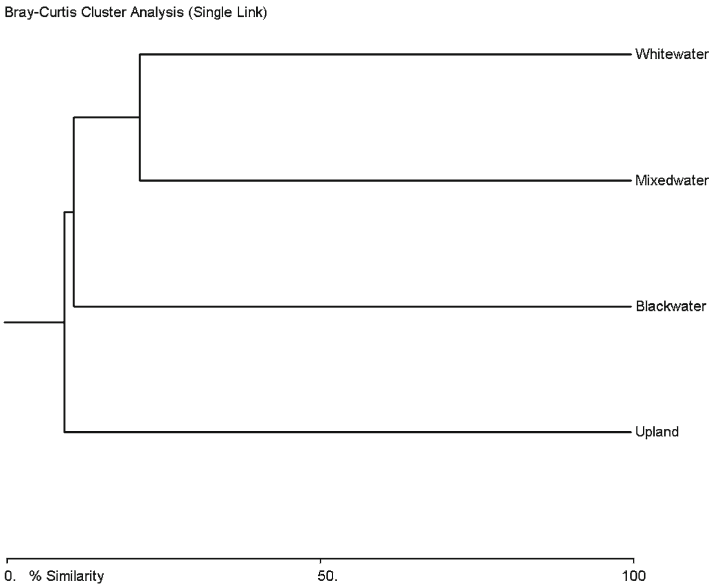

Fig. 16.8 Species similarity (Bray-Curtis; %) of Coleoptera between four forest types, evaluated from the canopy in Central Amazonia

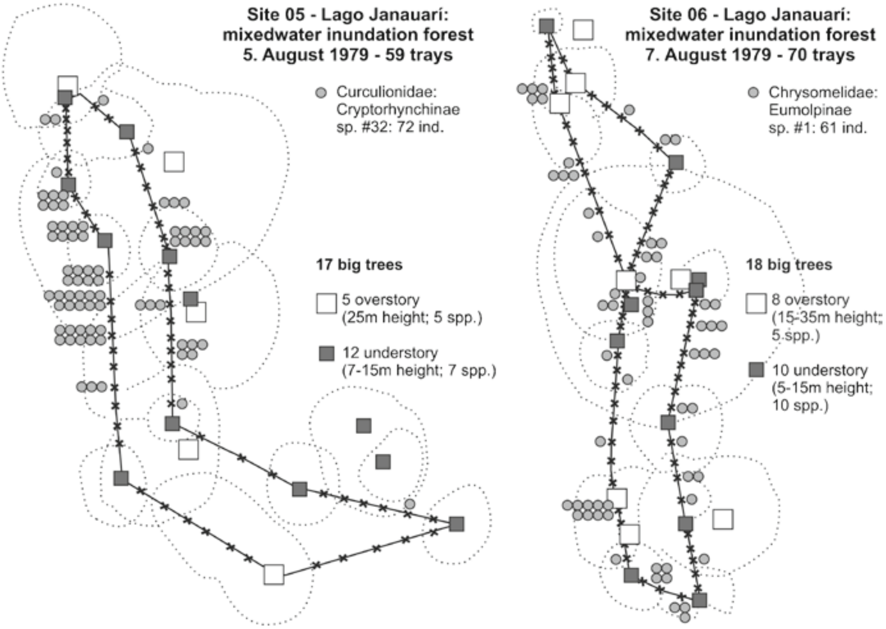

Fig. 16.9 Aggregated distribution of two dominant beetle species evaluated from the canopy of a mixedwater inundation forest in Central Amazonia along two selected transects

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).

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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Part III
Sustainable Management of Amazonian Floodplain Forests

Chapter 17
Wood Anatomy and Tree-Ring Structure and Their Importance for Tropical Dendrochronology

Martin Worbes and Esther Fichtler

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Abstract 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.

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17.1 Introduction

Trees all over the world face periodically unfavorable growing conditions and consequentially respond with cambial dormancy due to the annual variation of either precipitation (drought stress), temperature (frost) or flooding (water stress). This results in the reduction of radial growth for days or months and in differing wood anatomical structures that appear as rings in the cross-section of the tree stems. Rings are annual, if the triggering climate factors, such as a dry period in most parts of the tropics, occur once a year (Worbes 1995). Understanding the past and current dynamics of the world's tropical rain forests is an important current challenge for ecologists. Annual tree-ring patterns represent a reliable basis that can be used in various ways to gain information on forest dynamics (Worbes et al. 1992; Brienen and Zuidema 2006a), tree ages (Worbes and Junk 1999) growth rates, climate reconstructions (Worbes 1999; Schöngart et al. 2004,) to estimate management criteria (Schöngart 2010) and changes in the C-stocks of above-ground coarse wood biomass (Schöngart et al. 2010).

In Amazonian floodplain forests, water level fluctuations result in annually alternating aquatic and terrestrial phases. During the aquatic phases of the soil, anoxic conditions hinder root respiration and water uptake. This induces leaf shedding in many tree species (cf. Parolin et al. 2010c) followed by cambial dormancy (Schöngart et al. 2002). The reduction of growth at the end of the growing period leads in many species to a visible change in the formation and differentiation of wood cells. In most obvious cases a clear differentiation is possible into 'earlywood' cells, formed when the growing period starts, and 'latewood' cells, formed later in or at the end of the growing period. The first hint to the annual nature of these growth zones was given by Gessner (1968), it was proven by means of radiocarbon dating (Worbes 1984) and is the basis for a wide range of applications.

In the following chapter, 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. The described wood-anatomical structures are to be found in tree species throughout the globe as well. Therefore this chapter is to exemplify the general characteristics of tropical tree-ring structures.

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

17.2 Anatomical Classification of Tree-Ring Structures

Macroscopically apparent growth structures become visible as rings in a cross-section as light/dark zones or bands on sanded discs. Here, the anatomical background of 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)

				Distinctiveness				
Family	Genus	Species	Author	In	Out	Density ($g*cm^{-3}$)	Wood structure	Origin
Annonaceae	*Annona*	*sp.*	L.	+	+	0.33–0.39	A, B	várzea
	Duguetia	*sp.*	A. St.-Hil.	+	+		A, B	várzea
	Duguetia	*uniflora*	Mart.	+	+	0.58	A	igapó
	Guatteria	*sp.*	Ruiz and Pav.	±	+		A, B	várzea
	Pseudoxandra	*polyphleba*	(Diels) R.E.Fr.	+	+	0.51	A	várzea
	Pseudoxandra	*sp.*	R.E.Fr.	+	+		A, B	várzea
Apocynaceae	*Anacampta*	*riedelli*	(Müll. Arg.) Markgr.	–	–		A	igapó
	Bonafousia	*tetrastachya*	(H.B. and K.) Markgr.	±	–		A	várzea
	Malouetia	*furfuracea*	Benth. ex Müll. Arg.	–	–		?	igapó
Aquifoliaceae	*Ilex*	*inundata*	Benth. ex Reissek	±	±	0.43	A (B)	várzea
Bignoniaceae	*Crescentia*	*amazonica*	Ducke	+	+	0.41	A, B, C	várzea
	Tabebuia	*barbata*	(E. Mey.) Sandwith	±	+	0.76–1.0	A, B, C	igapó
	Tabebuia	*barbata*	(E. Mey.) Sandwith	+	+	0.53–0.85	A,B	várzea
Boraginaceae	*Cordia*	*sp.*	L.	+	±	0.35–0.39	A	várzea
Capparaceae	*Crateva*	*benthamii*	Eichler	+/±	±	0.39–0.48	A, B	várzea
Chrysobalanaceae	*Chrysobalanus*	*sp.*	L.	–	–	0.95	C	igapó
	Licania	*heteromorpha*	Benth,	±	+	0.9	C	igapó
	Licania	*sp.*	Aubl.	–	±, –	0.78*	C	igapó
Clusiaceae	*Caraipa*	*paraensis*	Huber	–	–	0.76	A, D	igapó
	Garcinia	*macrophylla*	Mart.	±	±	0,72*	A, C	várzea
Connaraceae	*Rourea*	*sp.*	Aubl.	+	+	0.65	A	várzea
Euphorbiaceae	*Amanoa*	*oblongifolia*	Müll. Arg.	–	±	0.76	C	igapó
	Hevea	*guianensis*	Aubl.	+	+	0.4	A, B, C	igapó
	Mabea	*nitida*	Spruce ex Benth,	±	±	0.61		igapó
	Margaritaria	*nobilis*	L. f.	+	+	0.65	A, B	várzea
	Piranhea	*trifoliata*	Baill.	+	+/±	0.83–0.93	B, C	várzea

(continued)

Table 17.1 (continued)

Family	Genus	Species	Author	Distinctiveness In	Distinctiveness Out	Density (g*cm^{-3})	Wood structure	Origin
Humiriaceae	*Humiriastrum*	*cuspidatum*	(Benth.) Cuatrec.	±	±		A	igapó
Lamiaceae	*Vitex*	*cymosa*	Bert. ex Spreng.	+/±	+/±	0.58–0.59	A	várzea
Lauraceae	*Endlicheria*	*arunciflora*	(Meisn.) Mez and C.K. Allen	+	+	0.63–0.82	A	igapó
	Nectandra	*amazonum*	Nees	+	+	0.39–0.47	A	várzea
Lecythidaceae	*Eschweilera*	*albiflora*	Miers	±	±	0.75	C	várzea
	Eschweilera	*sp.I*	Mart. ex DC.	+	+	0.55–0.67	C	várzea
	Eschweilera	*sp.II*	Mart. ex DC.	±	+	0,71–0,91*	C	igapó
	Eschweilera	*sp.III*	Mart. ex DC.	±	±	0,71–0,91*	A, C	igapó
	Jugastrum	*sp.*	Miers	+	+	0.71	C	igapó
Fabaceae	*Aldina*	*latifolia*	Benth.	–	–		A	igapó
	Macrolobium	*acaciifolium*	Benth.	±	+	0.42–0.49	A, B	várzea
	Macrolobium	*acaciifolium*	Benth.	±	+		A, B	igapó
	Parkia	*auriculata*	Spruce ex Benth,	+	+	0.65	A, B	igapó
	Poecilanthe	*amazonica*	(Ducke) Ducke	±	+	0.94	A, B	igapó
	Pterocarpus	*amazonum*	(Benth.) Amshoff	+	+	0.33	A, B, C	várzea
	Swartzia	*argentea*	Spruce ex Benth,	±	+		B, C	igapó
	Swartzia	*laevicarpa*	Amshoff	±	+	0.56–0.64	A, B, C	igapó
	Swartzia	*macrocarpa*	Spruce ex Benth,	±	±	1,02*	B, C	igapó
	Swartzia	*polyphylla*	DC.	±	+	0.56	A, B, C	igapó
	Swartzia	*sp.I*	Schreb.	–	±	1,02*	B	igapó
	Swartzia	*sp.II*	Schreb.	±	±	0.99	A,B,C	várzea
	Swartzia	*sp.III*	Schreb.	+	+	1,02*	A, B, C	várzea
	Tachigali	*sp.*	Aubl.	+	+	0.7	A	igapó
	Vatairea	*guianensis*	Aubl.	+	+	0.75	A	várzea
	Zygia	*inaequalis*	Pittier	+	±	0.62	A, B	várzea

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

(continued)

Table 17.1 (continued)

				Distinctiveness				
Family	Genus	Species	Author	In	Out	Density ($g*cm^{-3}$)	Wood structure	Origin
Violaceae	*Amphirrhox*	*surinamensis*	Eichl.	–	–		A	igapó
Vochysiaceae	*Erisma*	*calcaratum*	Warm.	±	±		C	igapó

Wood structure in respect of tree-ring delimitation: A = density variation, B = marginal parenchyma band, C = pattern of concurring parenchyma and fibre tissue and D = variation of vessel size and density. Combinations of A – D occur frequently. Density data marked with * originate from the Wood Density 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.

D. Often described for temperate tree species, but also occurring in tropical species, this type is characterized by varying frequency and diameter of vessels

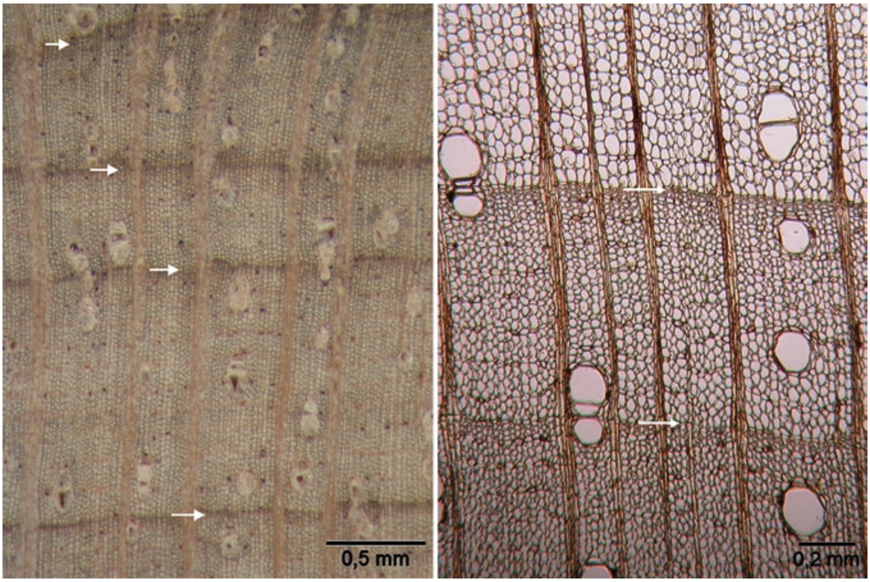


Fig. 17.1 Tree-ring type A, density variations in the wood structure of *Annona* sp., Annonaceae, in the várzea: (*left*) macroscopic and (*right*) microscopic cross-section

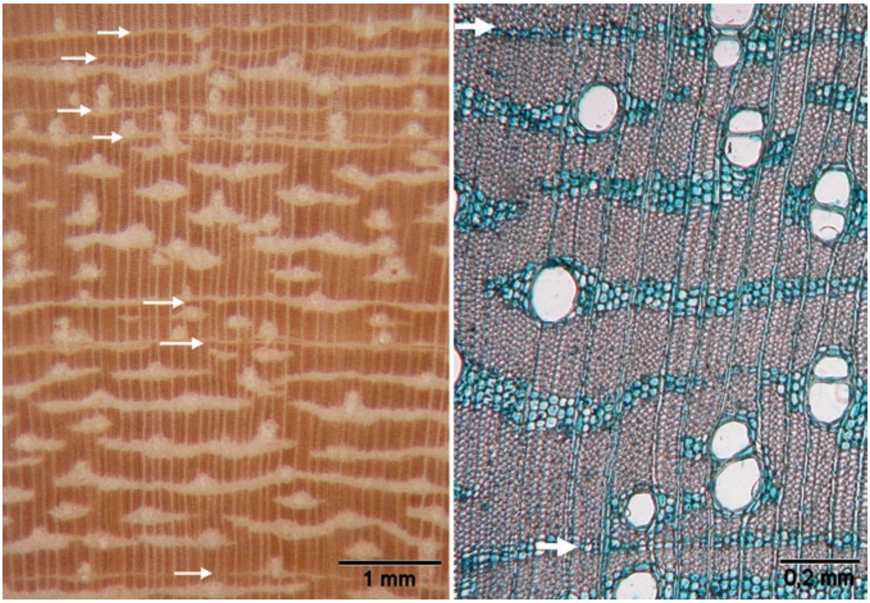


Fig. 17.2 Tree-ring type B, marginal parenchyma band in the wood structure of *Swartzia argentea*, Fabaceae, in the igapó, (*left*) macroscopic and (*right*) microscopic cross-section

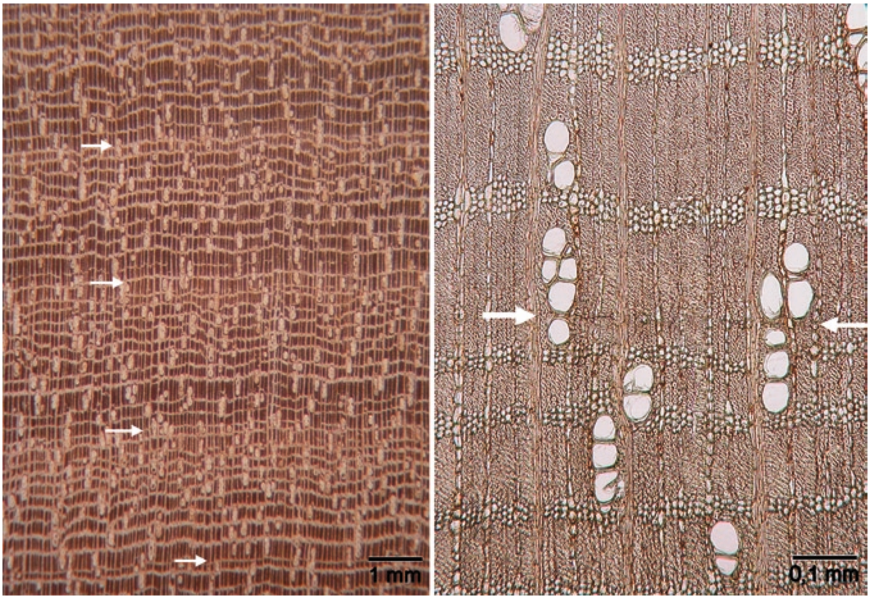


Fig. 17.3 Tree-ring type C, patterns of parenchyma and fibre bands, in the wood structure of *Pouteria glomerata*, Sapotaceae, in the várzea, (*left*) macroscopic and (*right*) microscopic cross-section

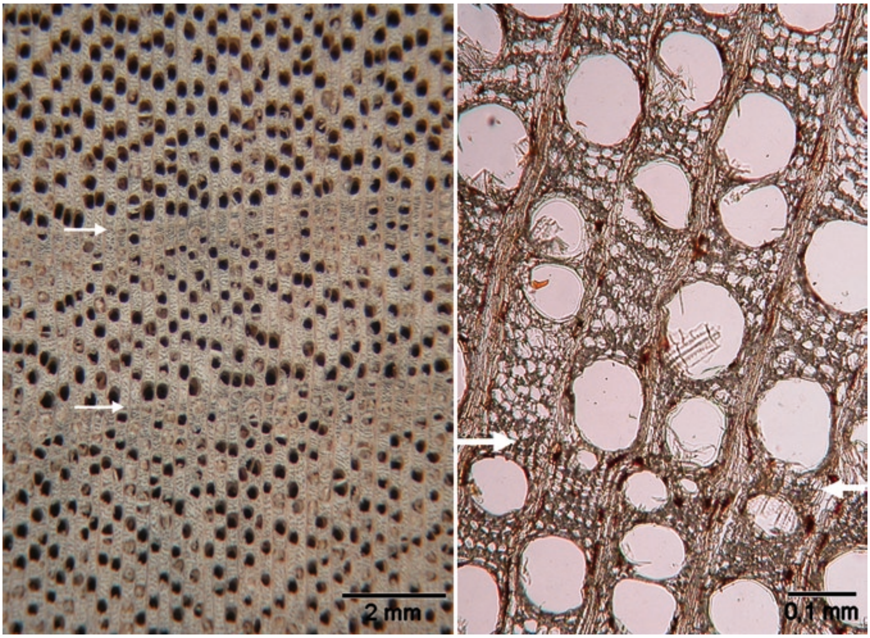


Fig. 17.4 Tree-ring type D, variation in vessel density/size in the wood structure of *Pseudobombax munguba*, Bombacaeae, in the várzea, (*left*) macroscopic and (*right*) microscopic cross-section

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 growth structure rather than searching for a single specific character delineating a tree ring.

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

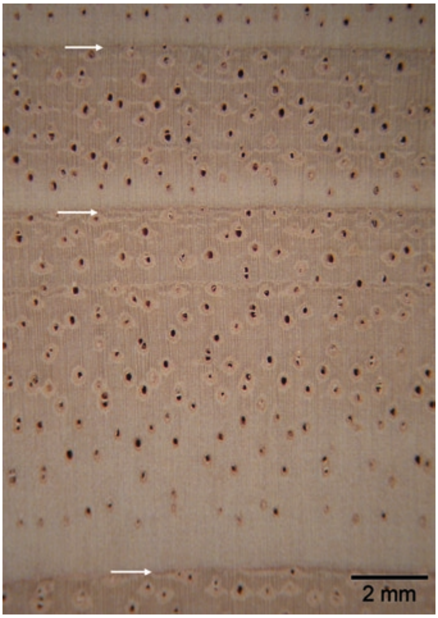
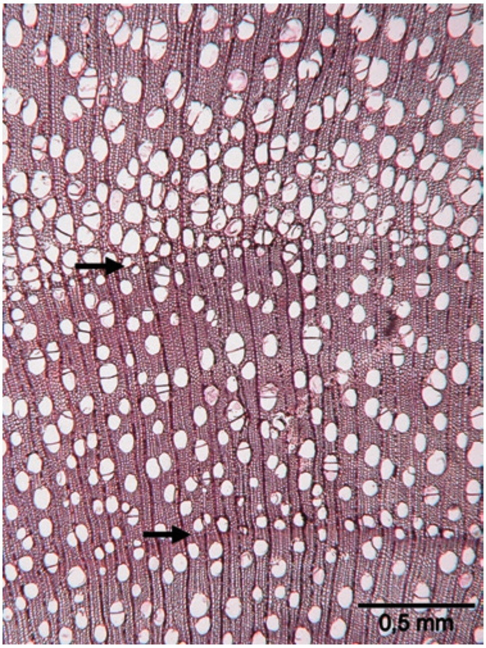


Fig. 17.6 Differing tree-ring boundaries of *Salix martiana*, Salicaceae, in the várzea showing variations in cell wall thickness (Type A) in one ring (*below*) and variations in vessel density/size (Type D) in a consecutive ring



17.3 Macroscopical Variability of the Visibility of Rings within Species and Individuals of Trees in the Igapó and Várzea

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.

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 species, individuals with clear concentric rings may occur as well as those with

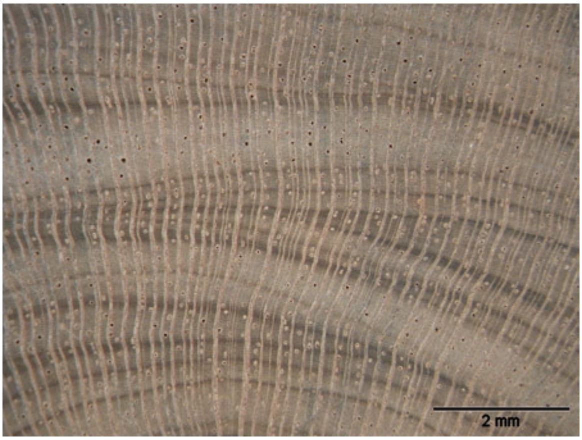


Fig. 17.7 Section of a disc of *Duguetia uniflora*, Annonaceae, in the igapó showing multiple wedging rings on various positions of the disc

frequently wedging rings. Within a stem disc, rings may tend to wedge only in outer parts, when the tree starts to form buttresses (Fig. 17.8).

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

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

In general, both floodplain forests produce trees with ring structures suitable for tree-ring analytical studies. Continuous as well as abrupt fluctuations of endogenous and exogenous factors result in structural changes of the wood anatomy and changing tree-ring widths. In dendrochronological studies abrupt changes are of special interest, as these can be used to date and analyse the impact of certain incidents,

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

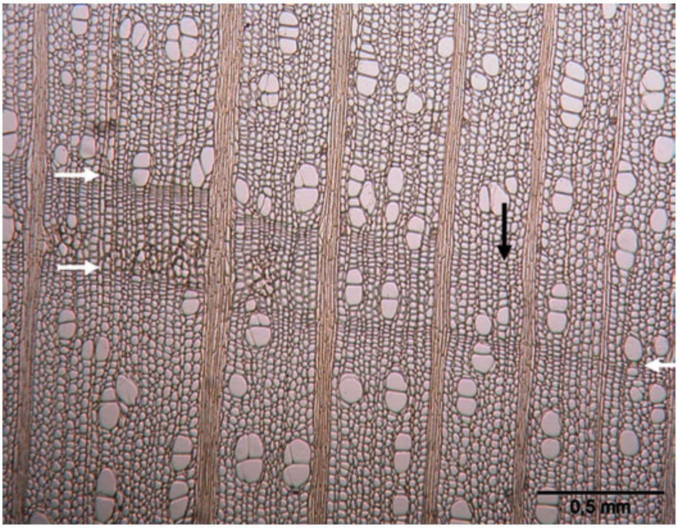


Fig. 17.9 Break-off of a tree-ring boundary in an individual of *Ilex inundata*, Aquifoliaceae, in the várzea. On the left site two, on the right site only one tree-ring boundaries are visible (*white arrows*), the black arrow roughly indicates the area where the boundary is not visible anymore

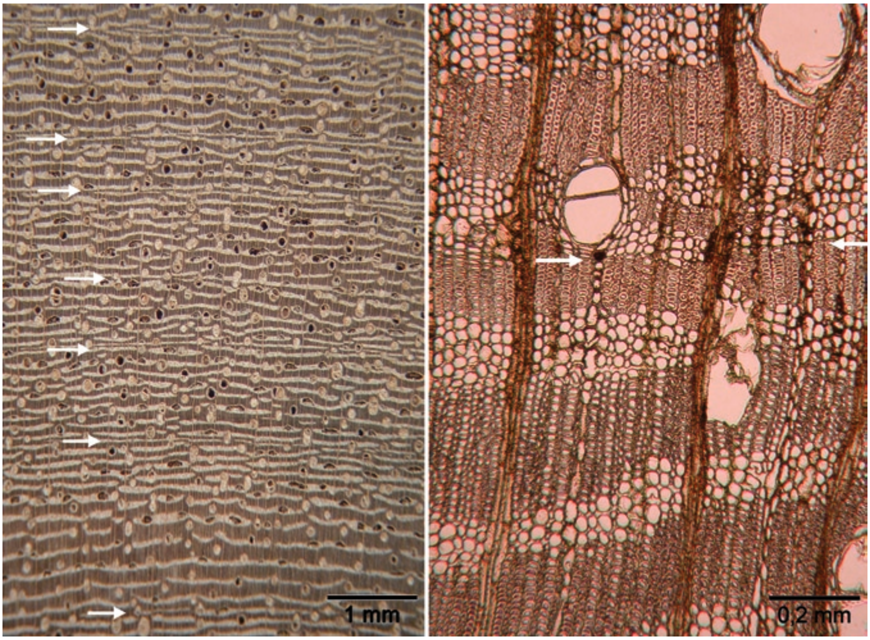


Fig. 17.10 Wood structure of *Erisma calcaratum*, Vochysiaceae, in the igapó showing generally ill-defined ring boundaries, (*left*) macroscopic and (*right*) microscopic cross-section; with increasing magnification the boundaries become more difficult to detect

such as extreme climatic events or suppression and release effects (Schöngart et al. 2004; Brienen and Zuidema 2006a).

17.4 Structure and Ecological Function of Xylem Elements in Growth Zones

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

Large variations occur in the share of parenchyma and fibres, suggesting large variation in storage capacities and mechanical stability. In different species of growth zone type C (cf. *Macrolobium acaciifolium* in Fig. 17.11) the absence of parenchyma and vessels in a broad band of fibres in the earlywood is obvious. This band is followed by a mixture of parenchyma, vessels and fibre wood in specifically dependent variations. Fink (1982) as well as Dünisch and Puls (2003) observed in different tropical tree species that starch is predominantly stored in axial parenchyma and soluble carbohydrates are mobilized at the beginning of the growing period in support of the formation of new leaves and secondary xylem before the new foliage produces carbohydrates through photosynthesis. That means, that the observed pattern in distribution of axial parenchyma and fibres is not random, but reflects clearly the mechanisms of carbohydrate storage and mobilization as a function of specific phenological behaviour triggered by the dominating and limiting external growth factor. The composition of the xylem, in general, exhibits large variations within and between trees. The image analytical comparison of two individuals of *Tabebuia barbata* from the várzea and the igapó, respectively, showed that also nutrient availability affects the relative share of parenchyma and fibres: The individual from the igapó showed smaller radial increments (1.17 mm) compared to the várzea tree (1.43 mm) and therefore invested more capacity in storage and mobilization by forming a large amount of axial (34.81%) and radial (11.23%) parenchyma compared to fibre cells (46.23%). That may help a tree to survive periods of low resource levels and thereby compensate low nutrient availability in the igapó (Schöngart et al. 2005). Given that fibre cells are the major costs of making xylem, it is not astonishing that the individual from the nutrient rich várzea can invest most in fibre cells (53.38%) and, as there is less need, fewer in axial (28%) and radial (7.96%) parenchyma.

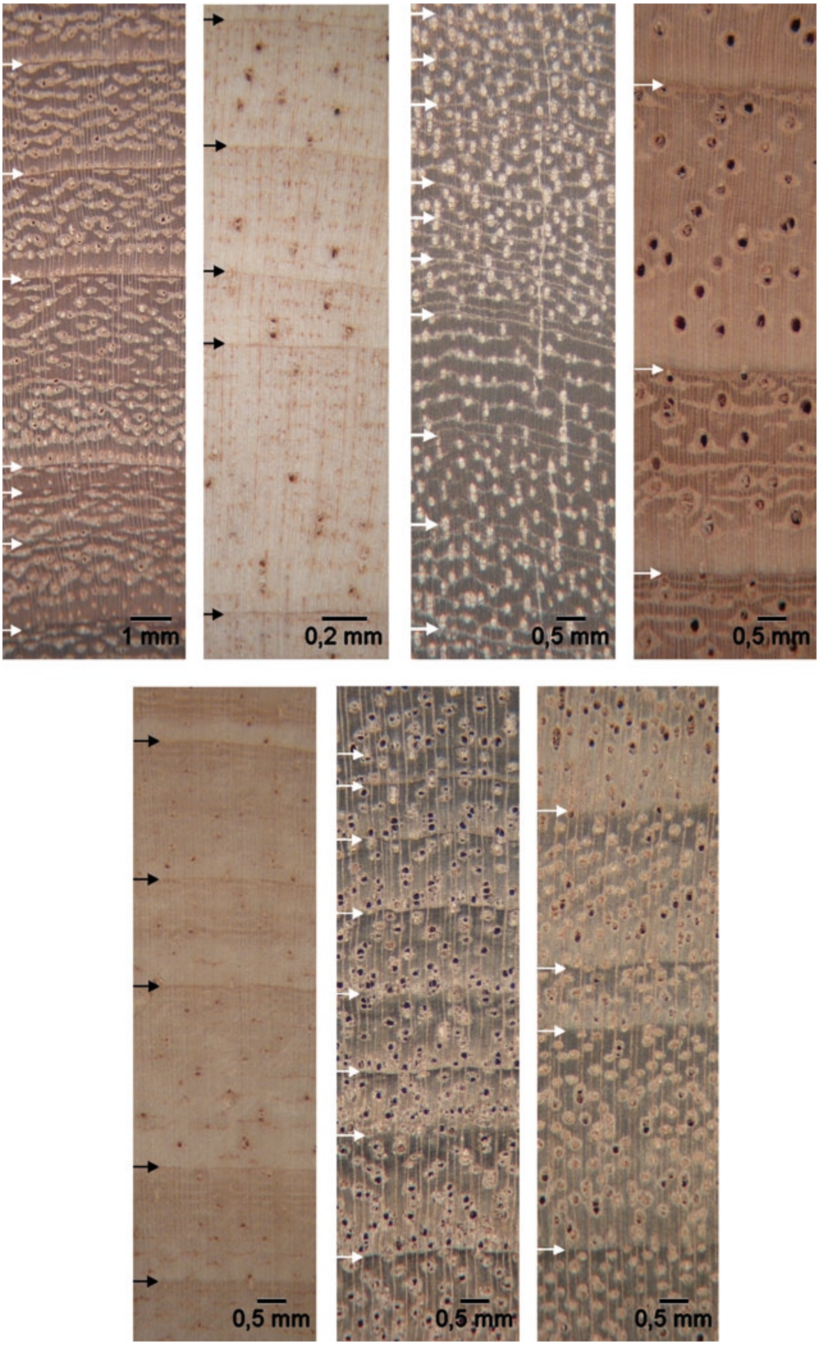


Fig. 17.11 Wood structure of tree species with distinct and continuous tree-rings boundaries: (from *left above* to *right below*) *Tabebuia barbarta*, Bignoninaceae, várzea; *Hevea guianensis*, Euphorbiaceae, igapó; *Piranhea trifoliata,* Euphorbiaceae, várzea; *Macrolobium acaciifolium*, Fabaceae, várzea; *Pterocarpus amazonum*, Fabaceae, várzea, *Endlicheria arunciflora*, Lauraceae, igapó and *Nectandra amazonum*, Lauraceae, várzea

17.5 How to Measure Growth Dynamics in Tropical Trees

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

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

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

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

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

Tree-ring analysis in tropical trees is not a new approach, but seldom used for applied purposes in the tropics. The annual nature of tropical tree rings is proven since the beginning of the twentieth century (Coster 1927). However, the huge diversity of tree species, wood structures and site conditions together with the still living paradigm that tropical trees never have annual rings, makes it necessary to prove the wood-growth periodicity of trees at many different sites. Again there are 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 et al. 2004, 2005), over lowland forests (Brienen and Zuidema 2005) to very dry sites (Fichtler et al. 2004; Schöngart et al. 2006) 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 to the inner parts of the stem (juvenile wood) as young trees in the tropics usually are influenced by strong competition and may show a different response to growth limiting factors compared to mature trees.

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

On this basis and under consideration of the above mentioned variations and peculiarities of the anatomical structures, tree-ring analysis can be used for a wide range of applications. Thereby special interest should be paid to gain realistic increment data for the implementation of sustainable management plans, reliable proxy data for tropical climate reconstruction and real tree ages for understanding forest and population dynamics. An example is the reconstruction of the Southern

Oscillation Effect (ENSO) with tree-ring data for the nineteenth century using the tree species *Piranhea trifoliata* in the várzea (Schöngart et al. 2004). An important discussion of academic interest as well as in the frame of carbon sequestration is the question of the maximum age of tropical tree species. In a review of recent literature on forest dynamics and carbon fluxes, the maximum age reported for the oldest tropical forest trees was found to increase rapidly among successive studies (Worbes and Junk 1999). These studies calculate or model the maximum age of tropical trees and tend to overestimate considerably (Condit et al. 1995), with the focus on the oldest theoretically possible age (Laurance et al. 2004).

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

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

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

Jochen Schöngart, Florian Wittmann, and Martin Worbes

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Abstract In this chapter the existing knowledge on biomass in floodplain forests and the compounds that contribute to their net primary production (NPP) are presented and discussed in comparison with data from non-flooded upland (terra firme) forests. Fine litterfall in old-growth floodplain forests are similar to litterfall data from terra firme forests. The few existing estimates of root biomass in nutrient-rich white-water floodplain forests (várzea) indicate lower belowground biomasses in floodplain forests than in terra firme forests due to regular flooding which limits the development of deep roots. Along the chronosequence, C-storage in the aboveground coarse live wood biomass (AGWB) of várzea forests indicates a strong increase during the first 50–80 years of successional development, but afterwards no increase in AGWB can be observed. On the other hand C-sequestration in the AGWB of várzea forests declines more than threefold along the successional gradient. In comparison to terra firme forest, the várzea forests have lower C-stocks,

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but a higher C-sequestration in the AGWB. The estimated aboveground NPP in young successional stages of the central Amazonian várzea is among the highest NPP known for tropical forests, while the NPP of the late succession in the várzea is in the upper range of the NPP of old-growth forests in the terra firme. The available database for nutrient-poor floodplain forests (igapó) is insufficient to estimate their NPP. Climate-growth relationships of tree-ring chronologies of species from central Amazonian terra firme and floodplain forests indicate opposing signals during El Niño years. During these events large areas of terra firme forests release carbon to the atmosphere due to the warmer and drier climate conditions, while the weakened flood-pulse favours tree growth in the floodplain forests which might therefore sequester parts of the climate-induced carbon emissions of terra firme forests.

18.1 Introduction

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.

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 = 10^{15} g or 10^9 t) for an area of 5.76×10^6 km^2 (Malhi et al. 2006). Based on more than 500 plot data and remote-sensing techniques, Saatchi et al. (2007) estimated a lower AGLB in the Amazon basin to be in the range of 59–73 Pg C for an area of 5.46×10^6 km^2. Floodplain forests comprise in this estimation an area of 328,825 km^2, with a total AGLB of 3.25 Pg C.

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

18.2 Fine Litterfall

The most frequently measured component of NPP is fine litterfall (Clark et al. 2001); however, in many studies it is not clearly stated what comprises fine litterfall, especially with respect to the wood fraction (bark, branches, twigs). Data on litterfall for

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

(Mg ha^{-1} year^{-1})	Low várzea	High várzea	*t*-value (p)
Leaves	4.76	5.21	24 (n.s.)
Other litter	1.62	1.62	0.98 (n.s.)
Total litter	6.39	6.84	0.74 (n.s.)

n.s. – not significant

Amazonian floodplain forests are available for the tidal várzea floodplains in eastern Amazonia (Cattanio et al. 2004), the central Amazonian várzea and igapó (Adis et al. 1979; Franken et al. 1979; Worbes 1997), and the Peruvian várzea (Nebel et al. 2001a).

During November 2002 and October 2003, fine litterfall (defined here as comprising leaves, fruits, flowers, and twigs up to 2 cm diameter) in permanent sample plots of late successional stages of low- and high-várzea forests was monitored in the Mamirauá Sustainable Development Reserve (MSDR) (Queiroz and Peralta 2010). Low várzea forests establish where the annual water column averages heights of more than 3 m, whereas high-várzea forests establish where it averages <3 m (Wittmann et al. 2002a,b; Wittmann et al. 2010). In both forests, ten quadratic traps, each with a surface of 1 m², were randomly distributed over a 1-ha area and litter was collected every two weeks. The various components of the litter were then separated and dry mass was determined after 72 h of drying at 75°C. Monthly litterfall was correlated with monthly water-level fluctuations (data: Mamirauá Institute for Sustainable Development, IDSM) and precipitation data of Tefé (National Institute of Meteorology, INMET).

Total litter fall in the low várzea was 6.39 Mg ha^{-1} year^{-1} (Megagram = 10^6 g) and in the high várzea 6.84 Mg ha^{-1} year^{-1} (Table 18.1). The difference in the 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,

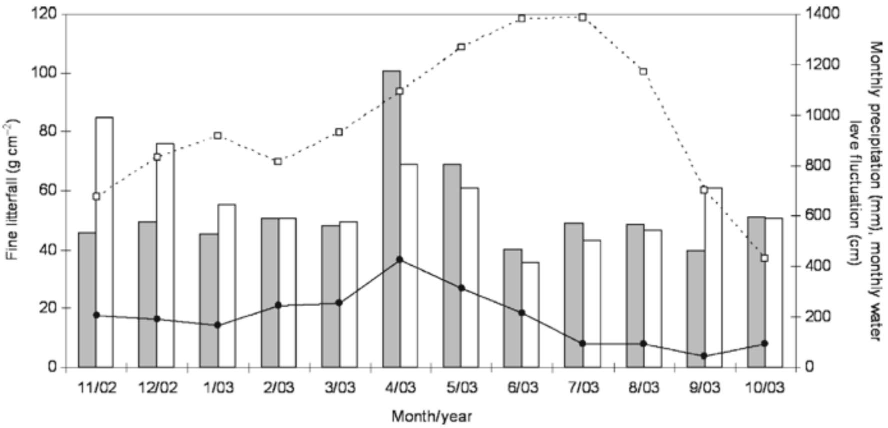

Fig. 18.1 Total fine litterfall in the low (*grey bars*) and high (*white bars*) várzea from November 2002 to October 2003 with respect to monthly rainfall (*black line*) (Data: INMET for Tefé-AM) and monthly water-level fluctuations of the Japurá River (*dotted line*) (Data: IDSM)

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

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

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).

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

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)

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 reported by Cattanio et al. (2004), who determined root biomasses in 24 holes, each with an area of 100 cm^2 and a depth of 100 cm, in tidal várzea forests (eastern Amazonia) of topographically low, intermediate, and high sites. Total root biomass increased along the flood-gradient, from 35 ± 4.8 at high elevations to 36 ± 8.1 Mg ha^{-1} at intermediate elevations and 40 ± 9.3 Mg ha^{-1} at low

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

Forest type	Root biomass (Mg ha^{-1})	Source
Várzea		
Eastern Amazonia (low tidal várzea, late secondary succession)	40 ± 9.3 (1-m depth)	Cattanio et al. (2004)
Eastern Amazonia (intermediate tidal várzea, late secondary succession)	36 ± 8.1 (1-m depth)	Cattanio et al. (2004)
Eastern Amazonia (high tidal várzea, late secondary succession)	35 ± 4.8 (1-m depth)	Cattanio et al. (2004)
Central Amazonia (low várzea, late successional stage)	8.5 (0.9-m depth)	This study
Central Amazonia (high várzea, late successional stage)	7.5 (0.9-m depth)	This study
Mangrove		
Taiwan	509.5 (1-m depth)	Komiyama et al. (1987)
Terra firme		
Puerto Rico (15–50 year-old secondary forests)	10.9–12.5 (1.0-m depth)	Lugo (1992)
Costa Rica (70-year-old secondary forests)	15.6 (0.85-m depth)	Berish (1982)
Venezuela (20-year-old secondary forests)	15.2 (0.7-m depth)	Saldarriaga et al. (1988)
Venezuela (30-year-old secondary forests)	16.7 (0.7-m depth)	Saldarriaga et al. (1988)
Venezuela (60-year-old secondary forests)	42.0 (0.7-m depth)	Saldarriaga et al. (1988)
Venezuela (80-year-old secondary forests)	17.2 (0.7-m depth)	Saldarriaga et al. (1988)
Venezuela, São Carlos (pristine forest)	132.0 (1.0-m depth)	Klinge and Herrera (1983)
Venezuela, São Carlos (pristine forest)	55.6–60.9 (0.5-m depth)	Stark and Spratt (1977); Sanford (1989)
Brazil, Manaus (pristine forest)	40.0 (0.5-m depth)	Klinge (1973)

elevations (Table 18.4). At all elevations, thick-root biomass (>2 mm diameter) and fine-root biomass decreased with increasing soil depth (Fig. 18.3). Worbes (1997) also found that root density increased along the flood gradient for central Amazonian várzea and igapó forests. Root density increased in the igapó from 19.9 × 10^3 km ha^{-1} at elevations flooded on average for 80 days to 35.7 × 10^3 km ha^{-1} at elevations inundated for 175 days mean aquatic phase. In the várzea, root density increases along the flood-gradient from 14.1 × 10^3 km ha^{-1} (110 days mean aquatic phase) to 18.0 × 10^3 km ha^{-1} (220 days mean aquatic phase). The higher root densities in the igapó may be related to the lower nutrient content of igapó soils compared to várzea soils (Meyer et al. 2010).

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

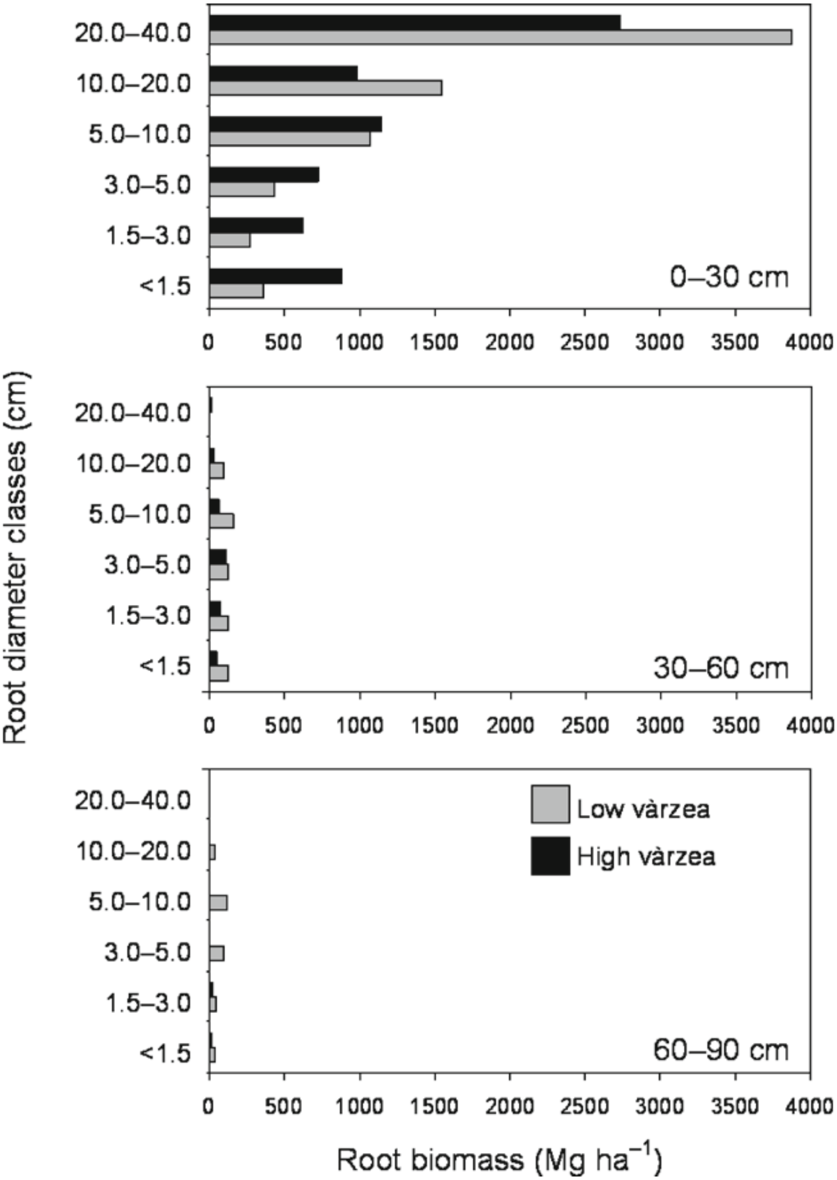

Fig. 18.2 Root biomass classified to different root diameter classes for soil layers 0–30, 30–60 and 60–90 cm in the low and high várzea of central Amazonia

In the igapó, fine-root production is mainly concentrated in the 0–20-cm soil layer. In the várzea root production is highest in the upper soil layer (0–15 cm) with a second maximum at a soil depth of about 40 cm, at the transition between clay and sand (Worbes 1997; Meyer et al. 2010). All studies in the floodplain forests indicate

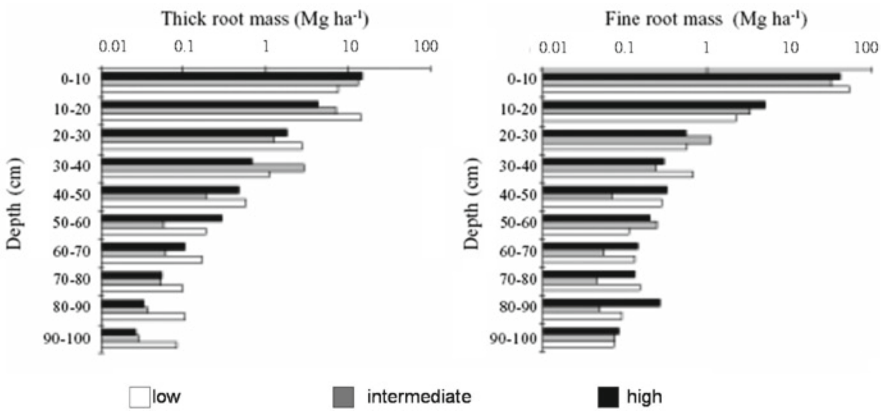

Fig. 18.3 Thick root biomass (>2 mm diameter) and fine root biomass (<2 mm diameter) in tidal várzea floodplains of different topographical elevations, classified by 10 cm soil layers (Cattanio et al. 2004)

increasing root biomasses and root densities with increasing length of the inundation period. This can be explained by the reduced period of root activity, which is mainly restricted to the terrestrial phase. A high root density is necessary for sufficient nutrient and water uptake during the relatively short growing period (Meyer et al. 2010).

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

18.4 Wood Density

Wood specific density (in g cm^{-3}) is a crucial key parameter for estimates of aboveground coarse live wood biomass (AGWB) and an important data for assessments of C-stocks and predictions of potential C-sequestration (Ketterings et al. 2001; Baker et al. 2004b; Chave et al. 2004, 2005). Wood density is also generally recognized as a reliable index of dead-wood decomposition (Martius 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 trees 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 2010). 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 (J. Schöngart, 2005, 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, aldheydes, 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 fibre contents and high vessel areas (>30%) (Worbes 1996); these result in low wood densities of 0.39 and 0.23 g cm^{-3}, respectively (Schöngart 2003). Late successional tree species such as *Piranhea trifoliata* (0.91 g cm^{-3}) and *T. barbata* (0.75 g cm^{-3}) have high wood densities due to their high fibre content (ca. 40%), thick cell walls, incorporation of numerous secondary substances, and relatively low vessel areas (<15%) (Worbes 1996).

In the várzea, mean wood density and standard deviation increase along the successional gradient (Worbes et al. 1992), from 0.30 ± 0.05 g cm^{-3} in a 6-year-old monospecific pioneer stand formed by *Cecropia latiloba* (J. Schöngart, 1998, unpublished data) to 0.70 ± 0.20 g cm^{-3} in a 240-year-old late successional stage containing 111 tree species ha^{-1} (Schöngart 2003) (Table 18.5). This difference can be explained by the substitution of pioneer tree species with low wood densities by late successional tree species with high wood densities along the successional gradient (Worbes et al. 1992). Low-density wood permits high radial increment rates, while high-density wood results in low increment rates. Thus, mean radial increment correlates negatively with wood density (Worbes 1996). Based on this relationship, Schöngart (2003) developed a non-linear regression model that predicts mean radial increments of várzea tree species by wood density (ρ) ($R^2 = 0.50$, $p < 0.01$) (Fig. 18.4). This approach allows age to be estimated on the basis of the tree diameter d as measured in the field and wood density ρ ($age = d/2 \times 1.3763\ \rho^{-1.2735}$).

One of the external factors determining wood density is interannual climate variation, as has been described for tree species growing in temperate and boreal zones (e.g., Schweingruber 1996). Worbes et al. (1995) used densitometry (Schweingruber et al. 1978) to show a significant relationship between the non-flooded period (vegetation period) and the maximum wood densities (latewood density) of the igapó species *Swartzia laevicarpa* ($r = 0.54$, $p < 0.05$) and of the várzea species *Pseudoxandra polyphleba* ($r = 0.55$, $p < 0.05$). It should also be noted that nutrient supply and light conditions result in different wood densities. Parolin et al. (1998) found that the wood densities of *Nectandra amazonum* and *T. barbata* were significantly higher in the nutrient-poor igapó than in young successional stages of the nutrient-rich várzea. The authors ascribed these differences to the lower increment rates of igapó species (Worbes 1997), which lead to higher wood densities and act as a special adaptation to the low nutrient content in the igapó (Parolin and Ferreira 1998). However, the comparison of wood density in trees of the same species but growing in different environments, i.e., young successional stages in the várzea and old-growth forests in the igapó, is problematic. Within the floodplain forests of the várzea, the diameter increment rates of *T. barbata* at the same tree age are about twice as high in young successional stages as in the late successional stage (Worbes et al. 2001), which can be explained by the larger amounts of relative photosynthetic active radiation (r*PAR*) in the young successional stage (Wittmann and Junk 2003) (Fig. 18.5). *T. barbata* has a significantly lower wood density in young successional stages than in old-growth forests with stand ages over 200 years, as indicated by a *t*-value of 4.59 ($p < 0.001$). No difference in the density of wood of same ages was found in *T. barbata* trees which grew under similar flooding regimes in old-growth forests of the várzea (0.80 ± 0.08 g cm^{-3}, $n = 20$) and the igapó (0.83 ± 0.08 g cm^{-3}, $n = 20$) (Fonseca Júnior 2007). For other tree species, however, this is not the case. Schöngart et al. (2005) reported that the wood densities of emergent trees of *Macrolobium acaciifolium* with similar diameters and growing under the same flooding conditions in old-growth forests were significantly lower in the igapó (0.39 ± 0.03 g cm^{-3}, $n = 20$) than in the várzea (0.45 ± 0.03 g cm^{-3}, $n = 20$)

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})
Várzea					
Martius (1992)	Lower Solimões River	4.00–5.50	20–40	13 (53)	0.49 (0.24–0.72)
Parolin et al. (1998)	Lower Solimões River	Varying	40–50	30 (177)	0.53 (0.22–0.87)
Schöngart (1998, unpublished data)	MSDR	6.00	6	1 (104)	0.30 (0.19–0.43)
Schöngart (2003)	MSDR	3.36	7	4 (38)	0.32 (0.21–0.54)
Schöngart (2003)	MSDR	3.47	19	15 (104)	0.35 (0.19–0.68)
Schöngart (2003)	MSDR	4.65	52	17 (110)	0.42 (0.18–0.82)
Schöngart (2003)	MSDR	4.14	125	77 (459)	0.60 (0.22–1.10)
Schöngart (2003)	MSDR	4.28	180	51 (133)	0.63 (0.30–1.11)
Schöngart (2003)	MSDR	3.36	240	34 (54)	0.70 (0.23–1.01)
Wittmann et al. (2006b)	MSDR	4.10	Late succession	30 (90)	0.62 (0.29–0.86)
Wittmann et al. (2006b)	MSDR	2.20	Late succession	30 (90)	0.57 (0.33–0.79)
Igapó					
Schöngart (2005, unpublished data)	Middle Negro River (Barcelos)	4.50	20	3 (30)	0.22 (0.14–0.34)
Schöngart (2004, unpublished data)	JNP	6.55	Late succession	7 (56)	0.60 (0.27–0.84)
Schöngart (2004, unpublished data)	JNP	4.10	Late succession	13 (65)	0.61 (0.29–0.97)
Schöngart (2004, unpublished data)	JNP	1.90	Late succession	14 (48)	0.67 (0.44–0.92)
Parolin and Ferreira (1998)	JNP/Tarumã mirím (Manaus)	Varying	Late succession	35 (206)	0.68 (0.40–0.86)
Parolin and Worbes (2000)	JNP	Varying	Late succession	27 (114)	0.67 (0.35–0.87)

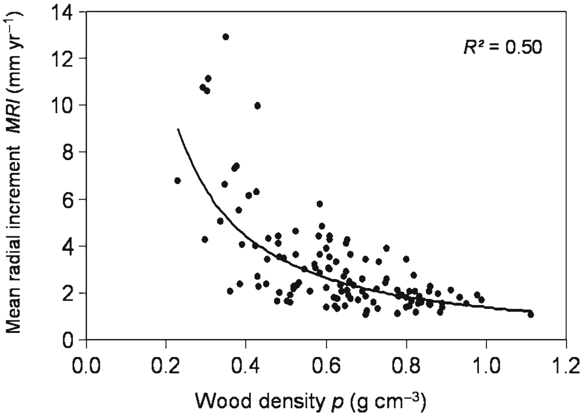

Fig. 18.4 Relationship between wood density and mean radial increment rates of 117 tree species in the várzea floodplain forests of central Amazonia (Schöngart 2003)

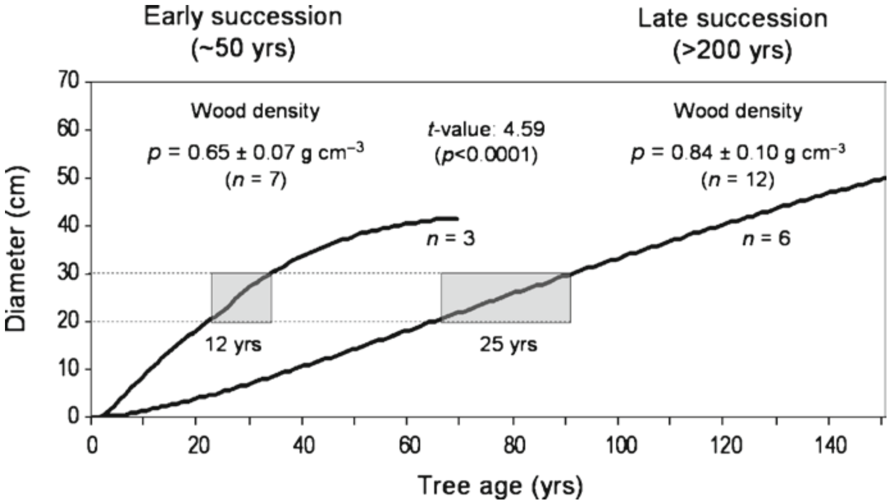

Fig. 18.5 Differences in the wood densities of *Tabebuia barbata* with fast growth rates in young successional stages and slow growth rates in a late successional stage. The grey boxes indicate the mean passage time to surpass a diameter class of 20–30 cm (Worbes 1994; Worbes et al. 2001; Schöngart 2003)

(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. 2010) 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. 2010c). 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 significantly lower wood densities in the várzea than in the igapó and terra firme (Table 18.6). Várzea floodplain forests are highly dynamic ecosystems characterized by intense sedimentation and erosion processes that annually create large new areas where pioneers start the primary succession (Worbes et al. 1992; Wittmann et al. 2002a,b, 2004). In igapó and terra firme forests, these processes depend on opportunities at much smaller spatial scales, such as the formation of small to

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

Forest type	Number of tree species	ρ (g cm^{-3})	*t*-test	*t*-value
Várzea (*v*)[a]	170	0.60 ± 0.15	*v* versus *i*	$t = -2.86, p < 0.01$
Igapó (*i*)[b]	73	0.66 ± 0.17	*v* versus *tf*	$t = -3.39, p < 0.001$
Terra firme (*tf*)[c]	696	0.65 ± 0.19	*i* versus *tf*	$t = 0.58, p = 0.28$

[a] Data from Martius (1992); Worbes et al. (1995); Worbes (1996); Parolin and Ferreira (1998); Schöngart (2003); (Wittmann et al. 2006b)

[b] Data from Worbes (1994); Parolin et al. (1998); Parolin (2002b); Schöngart (unpublished data)

[c] Data from Brown (1997); Fearnside (1997); ter Steege (2000); Baker et al. (2004b)

medium gaps caused by lightning, microburst of wind, disease, pest or age-related mortality; catastrophic destruction over large areas, common in some other forest formations, are rare. Due to such intensely dynamic processes, the proportion of pioneer tree species of the total species pool is much higher in the várzea than in the igapó and the terra firme, which explains the lower mean wood density of várzea tree species compared to those of the igapó and terra firme.

18.5 Aboveground Coarse Wood Biomass (AGWB)

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

In this section we examine 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. 2010). 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 2010), 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 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

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)

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

* Volume was estimated multiplying the basal area by tree height and a form factor of 0.6

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

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 (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 (ρ/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 (7) 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 ± 0.16 g cm^{-3} (Brown 1997) but a considerably lower value was determined for the young pioneer and secondary stages (0.32–0.42 g cm^{-3}; Table 18.7). Model (7), applied to describe a late secondary stage (50-year-old stand), produced particularly large errors due to the dominance in the canopy of low-density wood species, such as *P. munguba* (ρ = 0.23 ± 0.04g cm^{-3}), *Luehea cymulosa* (ρ = 0.38 ± 0.04 g cm^{-3}), and *Ilex inundata* (ρ = 0.39 ± 0.03 g cm^{-3}). These three species together comprised 66–69% (172–187 Mg ha^{-1}) of these

Table 18.9 Prediction of the AGWBs of five different successional stages in the várzea floodplain and three pristine forests in the igapó using allometric equations (1–7) (Table 18.8) (for description, see text)

Várzea	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Young pioneer							
Mg ha^{-1}	15	21	16	25	26	33	35
Mg m^{-2} basal area	1.1	1.5	1.2	1.8	1.9	2.4	2.6
Early secondary							
Mg ha^{-1}	108	127	117	102	128	171	217
Mg m^{-2} basal area	3.5	4.2	3.8	3.4	4.2	5.6	7.1
Late secondary							
Mg ha^{-1}	249	264	269	183	266	340	471
Mg m^{-2} basal area	4.9	5.2	5.3	3.6	5.3	6.7	9.3
Intermediate							
Mg ha^{-1}	222	228	240	169	240	305	239
Mg m^{-2} basal area	8.3	8.5	8.9	6.3	8.9	11.3	8.9
Late succession							
Mg ha^{-1}	233	233	251	174	257	307	253
Mg m^{-2} basal area	8.5	8.5	9.2	6.4	9.4	11.2	9.3
Igapó	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Low							
Mg ha^{-1}	68	85	74	99	115	155	94
Mg m^{-2} basal area	1.7	2.1	1.8	2.4	2.8	3.8	2.3
Medium							
Mg ha^{-1}	333	362	360	272	356	485	393
Mg m^{-2} basal area	7.0	7.6	7.5	5.7	7.5	10.1	8.2
High							
Mg ha^{-1}	240	257	259	188	246	324	235
Mg m^{-2} basal area	8.7	9.3	9.4	6.8	8.9	11.7	8.5

stands' AGWBs as estimated by models (1)–(3). The AGWB predicted by model (7) for these three species was twofold higher and accounted for 81% of the stand's AGWB. Estimations of AGWB generated by model (7) for stands >100 years old were similar to those produced by models (1)–(3), because of the similar mean wood densities of the successional stages. We therefore concluded that allometric models, which do not use ρ as a predictor, are biased towards errors in estimating the AGWB, due to the large variations in mean wood densities, especially of emergent trees, within and between stands. Baker et al. (2004a) and Malhi et al. (2004, 2006) used allometric equation (6) to estimate the AGWB of western Amazonian floodplain forests. Tree height, however, is not included in regression model (6), 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 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

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

	Basal area	AGWB	AGWB/Basal area
Várzea	m^2 ha^{-1}	Mg ha^{-1}	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

[a] Data from Almeida et al. (2004) of four 1-ha stands in the eastern Amazonian várzea

[b] Data from Worbes (1997)

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

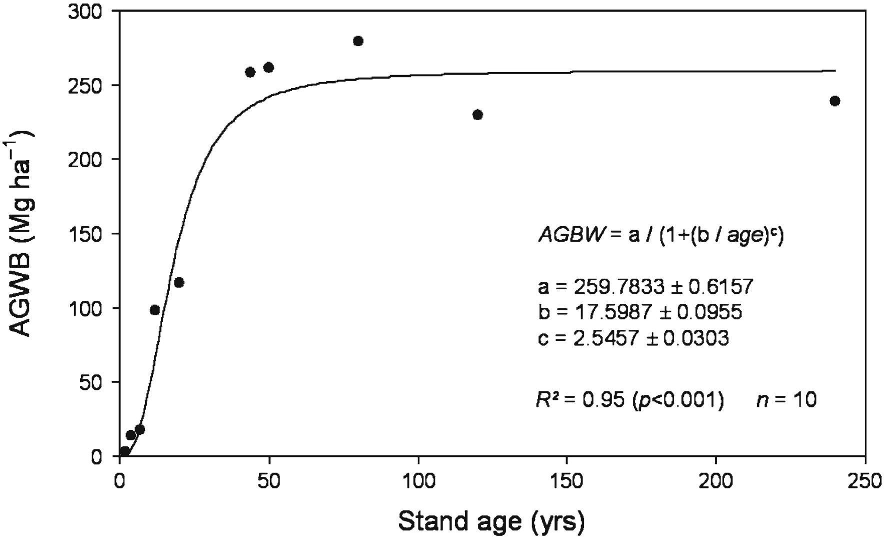

Fig. 18.6 Relationship between accumulated aboveground wood biomass (AGWB) and stand age along a successional gradient in the central Amazonian várzea

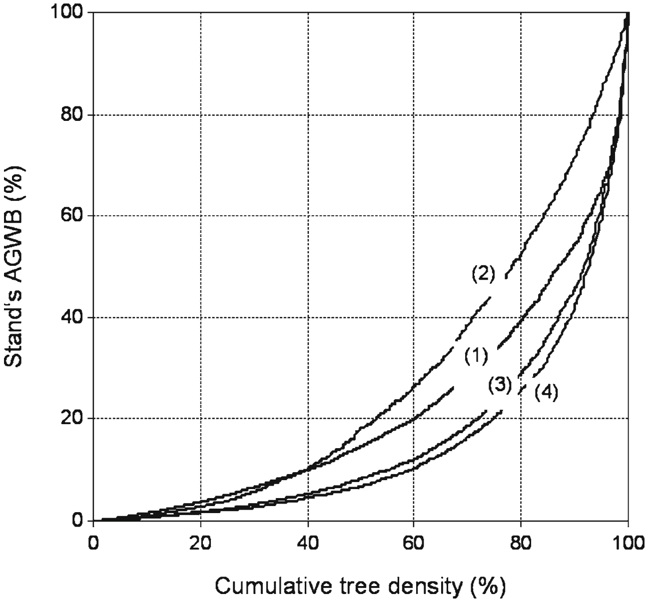

Fig. 18.7 Distribution of AGWB with respect to relative abundance in four 1-ha stands of varying stand age. 1 – 20-year-old early secondary stage, 2 – 50-year-old late secondary stage, 3 – 120-year-old intermediate stage, 4 – 240-year-old late successional stage

in 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. 1998) indicate that carbon stocks in Amazonian non-flooded upland forests (terra firme) have increased over the last decades, probably due to increasing atmospheric CO_2 concentrations. Other recent studies, however, showed that the increasing temperature and/or reduced soil moisture associated with the El Niño phenomenon (e.g., Tian et al. 1998; Cox et al. 2000; Clark et al. 2003) turn tropical forests into net carbon sources. A basin-wide estimate indicated that the biomass of floodplain forests (153,000 km²) is a C-sink of, annually, 15 × 10^{12} g C (Grace and Malhi 2002), corresponding to 0.98 Mg C ha^{-1} $year^{-1}$. Baker et al. (2004a) estimated a net C-sequestration of 1.27 ± 1.27 Mg C ha^{-1} $year^{-1}$ in three mature várzea forests of the western Amazon basin, observed during a 4–5-year period. We estimated annual C-sequestration in the AGWB along the entire successional gradient, from early secondary stages to old-growth forests in the MSDR. For these estimates, we applied growth models based on tree-ring analyses of the dominating tree species and species groups (Schöngart 2003). Our field data were extrapolated to a regional scale by remote-sensing techniques of Landsat TM image data (Wittmann et al. 2002a,b). In the following, the function of the AGWB in the várzea floodplains as a C-sink is discussed, in the light of data from terra firme forests.

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

$$d = \mathrm{a} / \left(1 + \left(\mathrm{b} / age\right)^{\mathrm{c}}\right) \tag{18.1}$$

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

$$CDI = d_t - d_{t-1} \tag{18.2}$$

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

$$h = d \times \mathrm{a} / \left(d + \mathrm{b}\right) \tag{18.3}$$

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

With these models, AGWB was estimated for every year by allometric equations (1–3), using diameter, tree height, and wood density. We estimated the C-content of AGWB to be 50% for slow-growing tree species in mature forests (Clark et al. 2001; Malhi et al. 2004) and 45% for fast-growing tree species of young successional stages. The wood of this latter group is characterized by fewer stable carbon compounds (e.g., lignin) in comparison to densewood tree species (Elias and Potvin 2003).

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})
	n	**a**	**b**	**c**	***r* (*p*)**	***n***	**a**	**b**	***r* (*p*)**	
Short-living pioneers										
Alchornea castaneifolia	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
Salix martiana	90	51.0618 ± 18.3017	12.1897 ± 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
Cecropia spp.	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
Cecropia latilobaCecropia membranacea										0.25 ± 0.01 0.30 ± 0.05
Cecropia sp.										
Ficus insipida	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
Nectandra amazonum	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
Rhodostemonodaphne sp.	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
Long-living pioneers										
Pseudobombax munguba	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
Luehea cymulosa	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
Ilex inondata	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

(continued)

Table 18.11 (continued)

Tree species / -group	Age-diameter relationship					Diameter–height relationship				Wood density ($g\ cm^{-3}$)
	n	**a**	**b**	**c**	***r* (*p*)**	***n***	**a**	**b**	***r* (*p*)**	
Macrolobium acaciifolium	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
Albizia subdimidiata										0.57 ± 0.05
Inga cf. *laterifolia*										
Sloanea excelsa	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)										
Pouteria elegans	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
Eschweilera parvifolia	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
Chrysophyllum argenteum										0.72 ± 0.08
Eschweilera albiflora	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
Tabebuia barbata	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
Piranhea trifoliata	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)										
Oxandra riedeliana	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
Mabea nitida	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
Duroia duckei	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

Myrtaceae spp.	2,659	70.8270 ± 32.7704	296.7414 ± 281.0952	0.8408 ± 0.1290	0.80 (<0.001)	299	26.6520 ± 0.5987	14.6247 ± 0.6777	0.94 (<0.001)	0.70 ± 0.07
Calyptranthes crebra										0.78 ± 0.05
Eugenia sp.										0.73
Marliera sp.										0.77 ± 0.10
Myrciaria dubia										
Licania spp.	1,101	164.0206 ± 53.9001	183.8475 ± 73.2115	1.4658 ± 0.1841	0.97 (<0.001)	62	38.3128 ± 0.2133	25.8947 ± 1.5740	0.95 (<0.001)	
Licania apetala										0.77 ± 0.12
Licania parvifolia										0.74 ± 0.08
Licania heteromorpha										0.80 ± 0.08
Discocarpus brasiliensis	1,204	60.3292 ± 26.5129	141.3601 ± 111.6131	1.0323 ± 0.2197	0.83 (<0.001)	72	38.1610 ± 2.557	27.8921 ± 3.1086	0.90 (<0.001)	0.79 ± 0.10

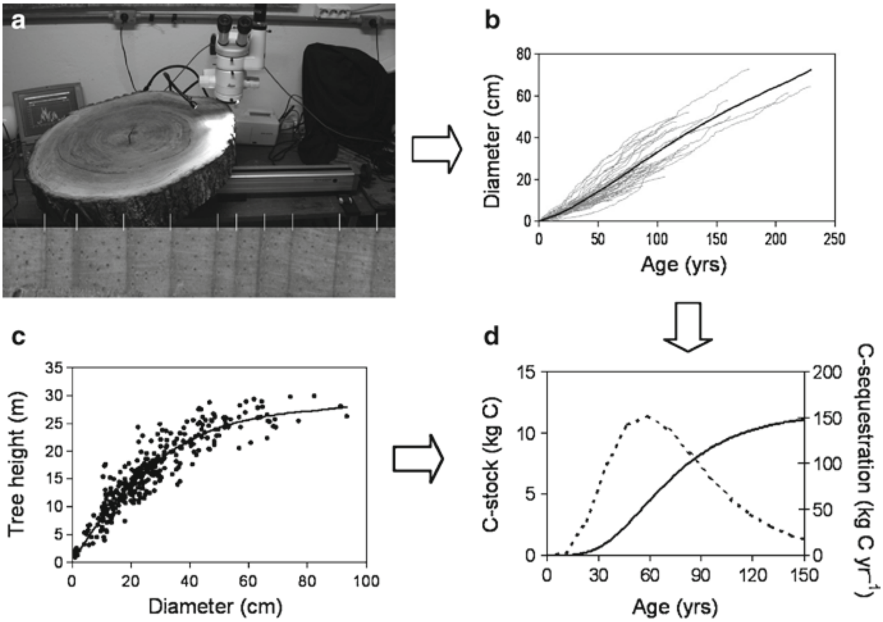

Fig. 18.8 Growth modelling based on tree-ring analyses: (**a**) Annual tree rings were analyzed on wood samples and ring-width was measured with a digital linear table (LINTAB) to (**b**) construct cumulative diameter growth curves for individual trees (*grey curves*) and a mean curve (*black curve*) 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*)

To estimate the carbon sequestration of a tree (kg year^{-1}), the difference between the C-stock in the AGWB of the year of the stand inventory (*t*) and that of the year before (*t–1*) was determined by the estimated diameter and height increments. The mean residence time of carbon in the AGWB (C-turnover) was calculated as the ratio C-storage/C-sequestration (Malhi et al. 2004).

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

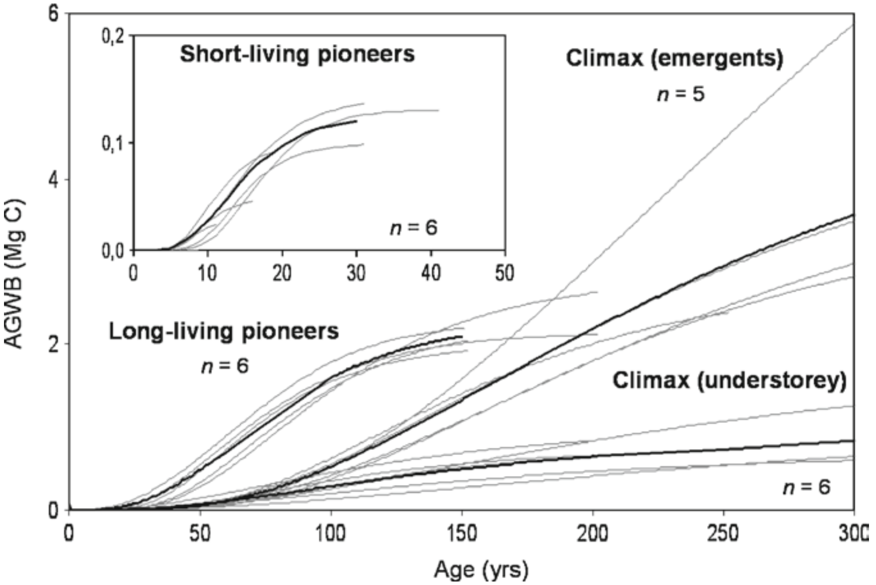

Fig. 18.9 Growth models of 23 tree species grouped according to growth type with respect to the accumulation of carbon in the AGWB. For every type, a mean growth curve is indicated (*black line*)

as Myrtaceae spp. is low. These growth models were used to estimate C-sequestration in AGWB according to allometric equations (1–3) 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.

Our results of C-storage in AGWB were much lower than those reported in other studies of nutrient-poor floodplain forests (igapó of clear-water rivers, Malhi et al. 2004) and of terra firme forests in central Amazonia (Chambers et al. 2001), the neotropics (Malhi et al. 2004), and the tropics worldwide (Clark et al. 2001). Our estimates of annual C-sequestration in the AGWB of várzea forests were lower than those of Nebel et al. (2001a) but similar to those of Malhi et al. (2004).

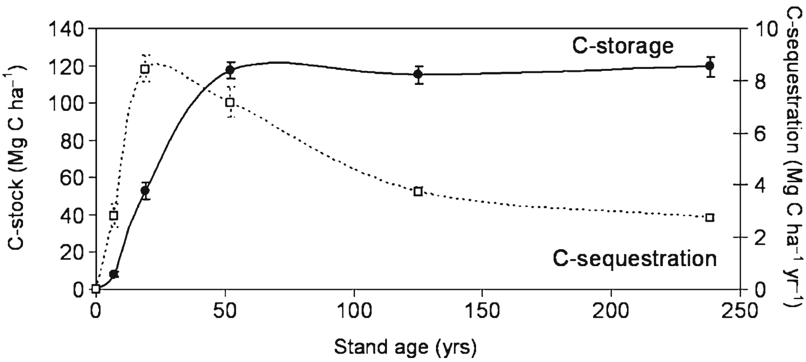

Fig. 18.10 Carbon stock (*black line*) and carbon sequestration (*dotted line*) in the AGWB along the successional gradient estimated by allometric equations (1–3)

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)

	C-storage (Mg C ha^{-1})	C-sequestration (Mg C ha^{-1} year^{-1})	C-turnover (years)
Source	Mean (minimum–maximum)	Mean (minimum–maximum)	Mean (minimum–maximum)
Várzea (white-water floodplain forests)			
This study (stand ages 7–240 years) (*n* = 5)	82.5 (7.9–119.5)	4.98 (2.73–8.45)	26
Nebel et al. (2001a) (*n* = 9)	198.4 (172.5–243.5)	7.43 (5.93–8.38)	27 (23–29)
Malhi et al. (2004) (soil class 7) (*n* = 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) (*n* = 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) (*n* = 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, *n* = 61)	146.3 (55.8–308.9)	2.66 (1.53–4.12)	57 (30–157)
Pantropics (Clark et al. 2001) (*n* = 39, *n* = 18)	139.0 (22.5–324.5)	1.90 (0.30–3.80)	56 (26–106)

Both studies were based on repeated diameter measurements in the várzeas of Peru and Bolivia (Table 18.12). In general, C-sequestration rates are lower in igapó forests and terra firme than in várzea forests. This can be traced to the better nutrient status of alluvial soils in the várzea (Furch 1997, 2000), which leads to higher diameter growth rates of várzea tree species than of igapó and terra firme tree species (Worbes 1997; Schöngart et al. 2005; Fonseca Júnior 2007).

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

	Land cover	C-storage		C-sequestration	
Forest type	ha	(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

Differences in canopy surface structure (canopy height, average and variation of crown sizes, aerodynamic roughness features) lead to different spectra in the RGB-scale of satellite images (Landsat TM, bands 3, 4, and 5) and permit the classification of forested areas in the MSDR into young pioneer and early secondary stages (coverage of 21,648 ha), late secondary stages (coverage of 71,094 ha), and climax stages (coverage of 92,004 ha) (Wittmann et al. 2002b). Up-scaling of the field data on C-storage and C-sequestration in the AGWB for different successional stages by multiplying those values with the estimated specific forest coverage resulted in a total C-storage of 19.8 × 10^6 Mg C and a total C-sequestration of 0.93 × 10^6 Mg C year^{-1} for the focal area of the MSDR, comprising 184,746 ha (Table 18.13). C-stocks in the AGWB of terra firme forests for an area of the same size as the forested focal area of the MSDR are 136–151% higher than in the várzea floodplain forests, based on the data of Chambers et al. (2001), Clark et al. (2001), and Malhi et al. (2004) (Table 18.13). C-sequestration in the AGWB of terra firme forests, however, is only 41–53% of that in the várzea. High C-storages and low C-sequestration rates in the AGWB of terra firme forests result in low C-turnover rates of 56–80 years. In the várzea floodplain forests, the mean C-turnover rate (mean residence time of C) in the AGWB is only 25.9 years (Table 18.12).

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) are in the same range as annual C-sequestration. Old-growth forests with stand ages >100 years have already reached equilibrium (steady state). Therefore, net C-sequestration in the AGWB in the várzea only occurs during the first 50–80 years of primary succession on newly deposited alluvial soils, reaching a maximum of approximately 5.31 Mg C ha^{-1} year^{-1} after about 17 years (Fig. 18.11). This observation is congruent with studies of forest recovery following complete clearance by humans for agricultural purposes (secondary succession), which have shown that

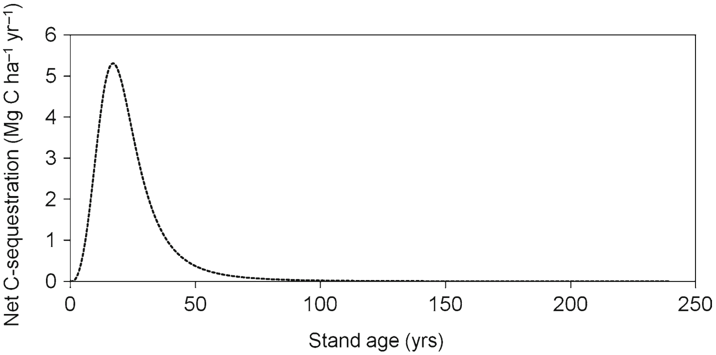

Fig. 18.11 Net carbon sequestration in the AGWB along the successional gradient estimated by alometric equations (1–3)

biomass approaches old-growth values after 80–100 years (Saldarriaga 1987; Fearnside and Guimarães 1996; Alves et al. 1997; Guariguata and Ostertag 2001; Vargas et al. 2008). Increasing stocks of AGWB in floodplain forests in the range of 0.62 Mg C ha^{-1} year^{-1} and 1.16 ± 0.39 Mg C ha^{-1} year^{-1}, reported by Phillips et al. (2008) and Baker et al. (2004a), respectively, were not confirmed by our data and might have been the result of overestimates of C-stocks and, consequently, of C-sequestration. Large C-stocks of AGWB are also lost through natural forest destruction caused by the lateral erosion and channel migration of rivers (Salo et al. 1986). Thus, net C-sequestration in AGWB during the first decades of primary succession may balance C-release from AGWB through natural forest destruction in the várzea, since the total forest cover in the várzea floodplains does not change over time (Fig. 18.12). Peixoto (2007) studied losses and gains of floodplains by erosion and sedimentation along the main channel of the Solimões and Japurá Rivers in the MSDR from 1984 to 2005 applying remote sensing techniques. During this period the floodplains lost 5.57% and gained 6.85% of its area resulting in net area increase of 1.27% corresponding to 3,300 ha or in average 157 ha year^{-1}.

We found significant correlations between C-sequestration in the AGWB and the structural parameters of the stand. The AGWB per m^2 basal area is linearly negatively correlated with C-sequestration (Malhi et al. 2006) ($r = 0.99$, $p < 0.01$). Our results showed that increasing AGWB m^{-2} basal area led to decreasing C-sequestration in the AGWB (Fig. 18.13). C-sequestration was also negatively correlated with crown coverage (m^2 ha^{-1}). Increasing crown coverage along the successional development (Schöngart 2003) corresponded to decreasing C-sequestration rates (Fig. 18.14). Surprisingly, C-sequestration in AGWB dropped along the successional gradient by almost 70% from the 20 year-old secondary stage to the 240 year-old stand. This strong decrease in C-sequestration can be explained by changes in species composition and in vertical canopy structure with increasing stand age. Along the successional gradient, tree height, individual crown size, and crown coverage per hectare increase (Terborgh and Petren 1991; Wittmann et al. 2002b; Schöngart 2003). In the 7-year-old young pioneer stage examined in this study, only 71% of the

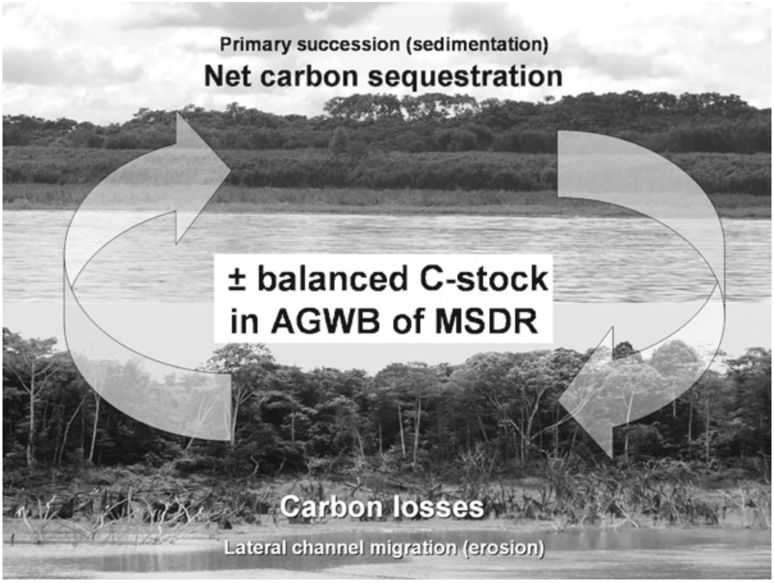

Fig. 18.12 In the várzea forest ecosystem net carbon sequestration in the AGWB occurs during the first 50–80 years of primary succession, which establishes on new deposited soils. On the other side C-stocks of AGWB get lost as a consequence of natural forest destruction caused by lateral erosion and 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

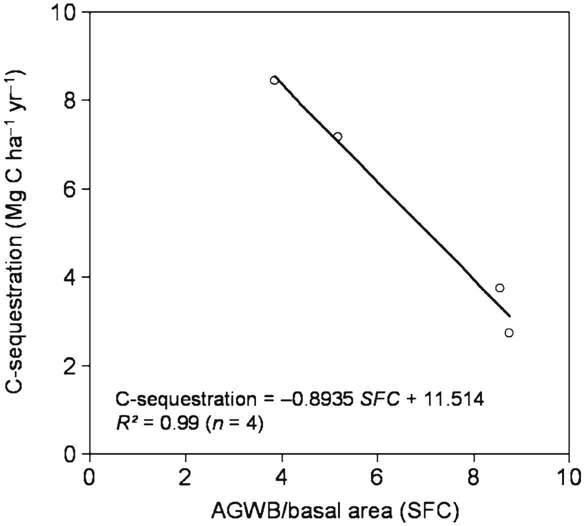

Fig. 18.13 Carbon sequestration as a function of accumulated AGWB per unit basal area, the structural conversion factor (SCF) (Malhi et al. 2006)

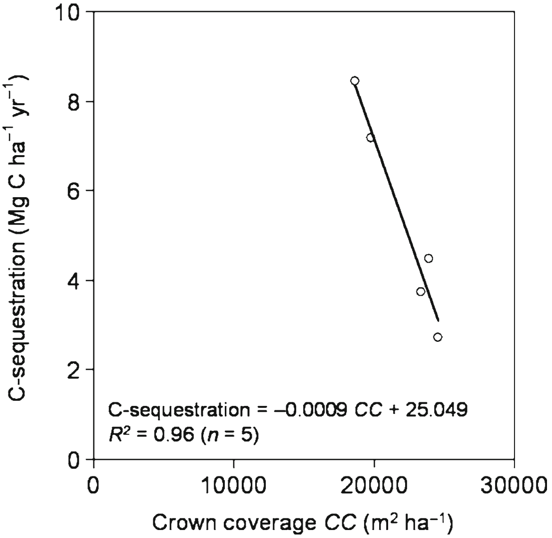

Fig. 18.14 Carbon sequestration in AGWB as a function of total crown area

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

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

area was covered by tree crowns, compared to 245% of the area of the 240-year-old late successional stage (Table 18.14). This corresponds to a decline of the r*PAR* measured above the forest floor, from about 31% r*PAR* in the 7-year old young pioneer stage to 4.6% r*PAR* in the late successional stage (Wittmann and Junk 2003). Despite the much higher crown coverage, the late successional stage absorbs only 25% more light than the young successional stages. In young successional stages, about 90% of tree crowns are exposed to sunlight compared to only about 40% in the late successional stage (Wittmann et al. 2002b; Schöngart 2003). Pioneer tree species forming the canopies of young successional stages have much higher net photosynthetic rates than climax tree species or understorey species (Table 18.15). The high crown areas in the lower and middle height classes of the canopy in the late successional stage exposed to low r*PAR* have low photosynthetic rates, but relatively high respiration rates to maintain important physiological processes (Horna 2002; Horna et al. 2010; Parolin et al. 2010a). This leads to lower C-sequestration in old-growth forests than in young successional stages.

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 (unterstory (*n* = 3 species)	2.6 (1.8–3.4)	0.23 (0.1–0.3)	2.4

[a]Net 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, aboveground 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 the short-lived (leaves, fine roots) carbon pool (Malhi et al. 2004). However, at some field sites, realistic data are available only for aboveground biomass increment and fine litterfall (Clark et al. 2001; Malhi et al. 2004), while other components of the ANPP and BNPP of tropical forests are lacking, insufficient or based on assumptions. Another problem is that most studies have no consistent methodology for calculating aboveground biomass increment and litterfall, which complicates comparisons between the NPPs of tropical forests and between forest ecosystems of other climates.

The ANPP of central Amazonian várzea floodplain forests was estimated by Worbes (1997). The value for 40–80-year-old successional stages near Manaus was

23.8–33.6 Mg ha^{-1} (11.9–16.8 Mg C ha^{-1}). For old-growth forests along the flood-gradient in the Peruvian várzea, Nebel et al. (2001a) reported an ANPP of 20.8 Mg 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 low várzea. However, methods of the two studies differed. Nebel et al. (2001a) estimated ANPP by the sum of the current biomass increment (derived from repeated diameter measurements during a 4-year period) and litterfall (including branches), while the estimate of Worbes (1997) was derived from the sum of fine litterfall (excluding branches), mean wood biomass increment, and dead wood. The latter method is problematic for two reasons. First, mean wood biomass increment was determined by total AGWB divided by stand age (Piedade et al. 2001), which is not equivalent to current AGWB production, derived by repeated diameter measurements or tree-ring analysis (Schöngart 2003). Second, for the estimate of ANPP, either dead wood (highly uncertain due to annually, periodically and episodically varying mortality, varying decomposition rates between tree species) or annual wood increment should be accounted, but not both (Nebel et al. 2001a). Dead wood can only be an estimate of wood biomass increments of forests that are in a steady state, which is not the case for young successional stages. Nebel et al. (2001a) predicted AGWB by estimated height, which, for the same forest type, were much higher than our measured tree heights. Repeated diameter measurements over short periods are problematic because of the imprecision in these measurements (Chave et al. 2004) as well as climate-induced growth anomalies (Clark and Clark 1994). The years 1993–1997 were characterized mainly by El Niño conditions and probably higher increment rates in várzea forests than in other years (Schöngart et al. 2004, 2005). Thus, the predictions of ANPP from Nebel et al. (2001a) may be biased towards overestimate.

Table 18.16 presents estimates of ANPP for three studied successional stages in várzea floodplain forests in the MSDR (Schöngart 2003) based on wood biomass increments and fine litterfall. Herbivory was estimated to be 10% of the litterfall, assuming that litterfall is made up, on average, of ~75% leaves (cf. Worbes 1997) and that 12% of this material is lost through herbivory (Clark et al. 2001). To account for additional losses through fruit and seed consumption, sap-sucking, and nectar-feeding by animals, we estimated total aboveground herbivory losses to be 120%

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)

[a] Data from Adis et al. (1979) for a 12-year-old successional stage (After Worbes 1997)

[b] Data from Adis et al. (1979) for a ~60–year-old successional stage (After Worbes 1997)

[C] This 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]					
n = 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]					
Pinus (19 years)	1.1	6.8	(0.8)	(0.3)	(9.1)
Swietenia (17 years)	3.3	5.6	(0.7)	(0.3)	(9.9)
Swietenia (40 years)	4.2	6.3	(0.8)	(0.3)	(11.5)
Secondary forests (Puerto Rico)[a]					
3–8 years (*n* = 1)	1.5	2.7	(0.3)	(0.3)	(4.8)
15–30 years (*n* = 2)	0.6–1.6	3.6–4.0	(0.4–0.5)	(0.3)	(5.4–6.0)
>50 years (*n* = 1)	1.3	5.3	(0.7)	(0.3)	(7.5)

[a] Data for NPP from Brown and Lugo (1992)

[b] Data for NPP from Clark et al. (2001)

of the leaf herbivory. VOCs, mainly isoprene and monoterpenes (Kesselmeier et al. 2002), were accounted for by the addition of 0.62 Mg ha^{-1} $year^{-1}$ (Guenther 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 and amount of the different VOC species. Kesselmeier et al. (2002) reported that 3.4–27% of the net ecosystem production (NEP = NPP – heterotrophic respiration) of tropical forests is released in the form of VOCs. Emissions of isoprenoids (isoprenenes, monoterpines) account for up to 2% of the NPP, but much higher values of 15–50% are reached under special conditions (Harley et al. 1999). Especially during the aquatic phase, which in the central Amazonian floodplain forests can last up to 270 days $year^{-1}$ at the lowest elevations (Junk 1989), other organic C-compounds, such as ethanol and acetaldehyde, are emitted in response to the anoxic conditions of the areas surrounding the roots (Rottenberger 2003).

Branch enclosure under greenhouse experimental conditions in which four different floodplain tree species were examined indicated a pronounced diurnal pattern in ethanol and acetaldehyde emissions, with maximum amounts released during the morning. This pattern was interpreted as arising from ethanol accumulation in the roots at night (Schlüter and Furch 1992), when the stomata are closed, and an emission as soon as the stomata open, due to the light-induced transpiration stream. Differences between ethanol and acetaldehyde emissions among tree species also have been observed (Parolin et al. 2004b). With this background, the Amazonian floodplain forests are of special interest because of the potential change in the emission levels in response to root anoxia, and may have even higher ANPPs than indicated.

18.8 Climate–Growth Relationships

For several tree species in the central Amazonian floodplains there is a negative correlation between the monthly increment rates and the mean water level (Schöngart et al. 2002). During the first half of the aquatic phase, diameter increment decreases to zero, indicating a cambial dormancy of at least 2 months during the flooding period, ultimately leading to the formation of the tree ring (Worbes and Fichtler 2010) (Fig. 18.15). Diameter growth starts again immediately after the flushing of new leaves and diameter increment rates remain high during the terrestrial phase. The sum of monthly increment rates during the vegetation period accounts for the width of the annual tree ring. Ring-width indices correlate significantly with the length of the terrestrial phase, as shown for *T. barbata* (Worbes 1989; Fonseca Júnior 2007), *P. trifoliata* (Schöngart et al. 2004), and *M. acaciifolium* (Schöngart et al. 2005). Thus, the yearly oscillation in ring width captures the interannual variation in the length of the terrestrial phase (Fig. 18.16). During El Niño years, basin-wide negative rainfall anomalies generally occur, leading to a weakened flood-pulse (Schöngart and Junk 2007) and an extension of the terrestrial phase (Schöngart et al. 2004). Trees in the central Amazonian floodplains respond to these anomalies by a significant increase in growth, as indicated in Table 18.18. In the adjacent non-flooded terra firme forests, however, tree growth is correlated with precipitation patterns (Worbes 1999; Dünisch et al. 2003; Brienen and Zuidema 2005). Tree-ring chronologies of *Cariniana micrantha* and *Eschweilera* spp. from central Amazonian terra firme forests correlate significantly with rainfall patterns (data: INMET for Manaus). A *t*-test indicated significantly lower ring-width indices during El Niño years than during other years and the opposite tree-ring pattern in the floodplain forests (Table 18.18).

The opposing climate-growth relationship between terra firme and várzea is important in the context of the interannual variation of carbon sequestration in the AGWB of adjacent Amazonian forests. The drier and warmer climate conditions 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

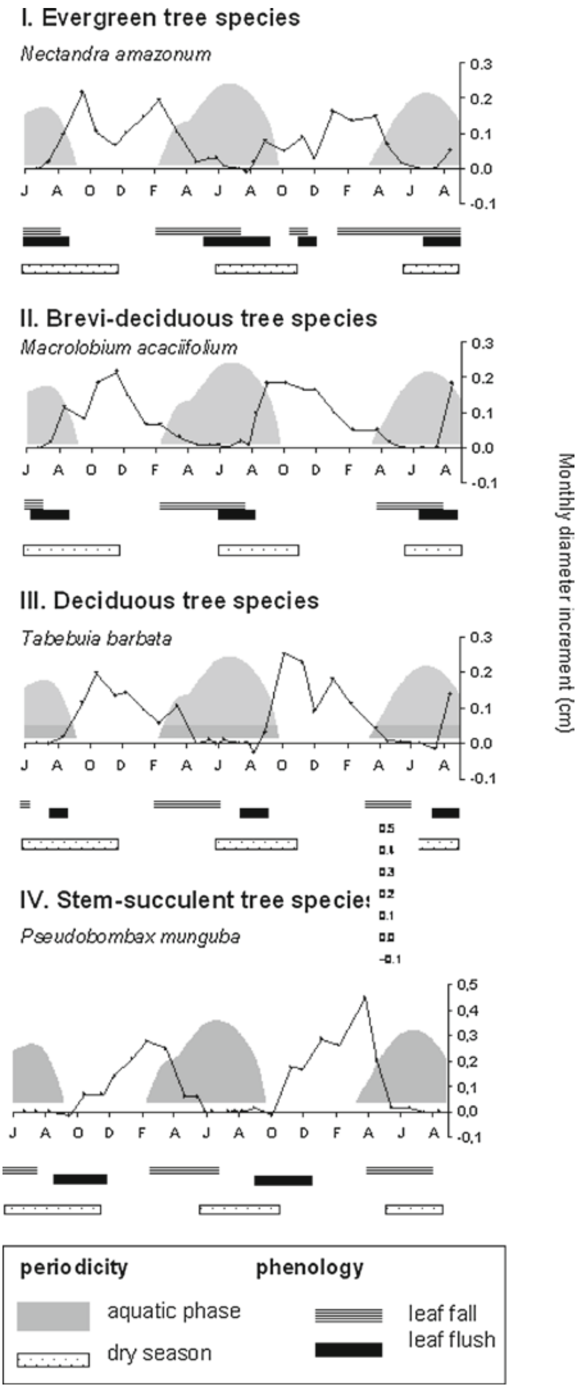

Fig. 18.15 Phenology and monthly variations in stem diameter increment derived from dendrometer measurements in a central Amazonian white-water floodplain forest for different ecotypes. The results are shown in relation to the flooded period and the dry season for the study period between June 1998 and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

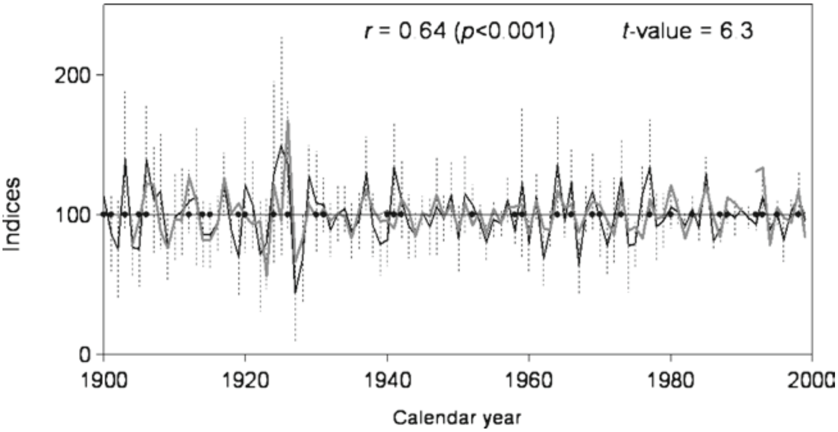

Fig. 18.16 Indexed ring-width chronology ($n = 10$ stem discs) of *Piranhea trifoliata* (*black curve*) and indexed time series of the duration of the non-flooded period (*grey curve*) derived from the daily recorded water level at the port of Manaus. The correlation between the two curves is significant.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

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

Ring-width index	*El Niño*-years	Other years	*t*-value
Terra firme			
1871–2002	$n = 44$	$n = 88$	
Eschweilera spp.[a]	95.0 ± 16.1	100.6 ± 19.4	−1.77 ($p < 0.05$)
Cariniana micrantha[b]	93.5 ± 18.8	102.3 ± 16.6	−2.68 ($p < 0.01$)
Várzea			
1871–1999	$n = 43$	$n = 85$	
Piranhea trifoliata[c]	104.2 ± 8.3	97.2 ± 8.9	4.26 ($p < 0.001$)
1871–2003	$n = 44$	$n = 89$	
Macrolobium acaciifolium[d]	106.7 ± 34.9	95.0 ± 32.2	1.85 ($p < 0.05$)
Igapó			
1871–2003	$n = 44$	$n = 89$	
M. acaciifolium[d]	107.4 ± 32.3	96.0 ± 35.8	1.81 ($p < 0.05$)

[a] Data from M. Sack (unpublished)
[b] Data from Funck (2004)
[c] Data from Schöngart et al. (2004)
[d] Data from Schöngart et al. (2005)

(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. 2010c), 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.

18.9 Conclusions and Outlook

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

- Fine litterfall in mature forests of the várzea and igapó does not differ significantly. Young successional stages have higher litterfall rates than old-growth forests in the várzea.
- Shallower rooting depths in floodplain forests lead to lower root biomasses than in terra firme forests.
- No differences in the wood density between old-growth forests in the várzea and igapó were found. The wood densities of old-growth floodplain forests are in the range of those of mature terra firme forests.
- Biomasses in the floodplain forests are lower than indicated by earlier estimates or measurements. C-stocks in the AGWB are much lower than in terra firme forests.
- Tree-ring analysis indicates that biomass productions in younger successional stages are much higher than indicated in earlier studies. By contrast, biomass production of old-growth forests in the várzea was found to be lower.
- New estimates of the ANPP for várzea forests of different successional development showed that young successional stages, which have an ANPP of 31.8 Mg ha^{-1} year^{-1}, are among the most productive tropical forests worldwide. The NPPs of old-growth várzea forest is in the range of terra firme forests. The database for estimates of BNPP is insufficient.

Results obtained as part of the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) have contributed to controversial discussions about the function of tropical forests as significant long-term carbon sinks (a.o., Grace et al. 1995; Malhi et al. 1998, 2004; Phillips et al. 1998, 2008; Clark 2002; Grace and Malhi 2002; Richey et al. 2002; Saleska et al. 2003; Ometto et al. 2005). Our results characterize várzea floodplain forests as highly dynamic ecosystems with low AGWB and high NPP, but also indicate variations of NPP and biomass for stands of different successional stages. Stand age is an important predictor and parameter for estimates of the components contributing to NPP, but in most studies no information 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 2010). 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 2010). 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 CO_2 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 CO_2 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 CO_2 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 CO_2 from canopy respiration, and CO_2 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-year 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.

Many studies have shown that sea surface temperatures (SSTs) in the tropical Pacific basin and tropical North Atlantic influence water-level fluctuations and discharge in the catchments of the Amazon rivers (Richey et al. 1989; Marengo 1992; Whetton and Rutherfurd 1994; Adis and Latif 1996; Amarasekera et al. 1997; Marengo et al. 1998, 2008; Coe et al. 2002; Foley et al. 2002; Aalto et al. 2003;

Schöngart et al. 2004; Ronchail et al. 2005; Harris et al. 2008). The El Niño-Southern Oscillation (ENSO) causes large-scale precipitation anomalies in the Amazon basin (Sombroek 2001), 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).

Two future scenarios with opposite trends may impact the flooding patterns of central Amazonia and thus affect tree growth. The first is that runoff and river discharge generally increase when natural vegetation (especially forest) is removed (Foley et al. 2005). In the light of future land-use scenarios for the Brazilian Amazon region (Soares-Filho et al. 2006), this will strongly impact the floodplain forests along the Madeira, Tapajós, Xingú, Tocantins, and Araguaia Rivers. For instance, the Tocantins River basin in Brazil showed a 25% increase in river discharge between 1960 and 1995, coincident with expanding agriculture in the catchment area, but no major change in precipitation (Costa et al. 2003). The second trend is a decrease in inundation length driven by increasing temperatures and CO_2 concentrations (Foley et al. 2002). The models of Costa and Foley (2002) predict a basin-wide decrease of precipitation and an increase in temperature as effects of deforestation, doubled CO_2 concentrations, and interactions between these processes. A temperature increase in the Amazon basin may exacerbate drought effects by accelerated evaporation (White et al. 1999). Severe droughts in terra firme forests provoked by El Niños such in 1925/1926 and 1997/1998 (Sternberg 1988; Sombroek 2001; Williams et al. 2005) caused CO_2 releases over large areas of Amazonian non-flooded terra firme forests (Prentice and Lloyd 1998; Foley et al. 2002) and increased the fire risk of these forests in areas experiencing high rates of selective logging and fragmentation (Nepstad et al. 1999). Large-scale fires, pastures, agriculture, and commercial logging all release huge amounts of greenhouse gases to the atmosphere (Laurance et al. 2001; Cochrane 2003; Asner et al. 2005), which feed back and accelerate climate changes (IPCC 2007) and probably increase the strength of the ENSO (Timmermann et al. 1999). The predicted increase in SSTs in the tropical Pacific and Atlantic (IPCC 2007) will probably lead to increased drought probability for the future (Malhi et al. 2008; Nepstad et al. 2008) and generally lower floods in the central Amazonian floodplain forests (Schöngart and Junk 2007; Marengo et al. 2008) and will probably affect forest dynamics and the carbon cycle in the AGWB of floodplain forests.

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Chapter 19
Use of Amazonian Floodplain Trees

Florian Wittmann and Astrid de Oliveira Wittmann

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Abstract Amazonian floodplain trees are used for a variety of purposes. Easy access to floodplain forests, the variety of timber and non-timber forest products (NTFPs), and especially the low cost of timber harvesting, processing and transport lead to an intense use of many floodplain tree species. Quantitative inventories in várzea forests indicate that up to 70% of all tree species are useful to the floodplain inhabitants and/or extractors. In Brazilian Amazonia, quantitative most important use category is timber for the construction of homes, boats, and floating houses, followed by phyto-medical extracts from trees, and edible fruits. Other uses each derived by few or even a single tree species might be of some economic importance when extraction occurs next to the markets. Although timber from up to 70 different várzea tree species is used for different purposes, timber extraction concentrates on comparatively few species. Most timber species occur in the high-várzea, and some of them already disappeared from local markets due to overexploitation. While the net present values of timber are easy to quantify, the value of some NTFPs to the inhabitants is indirect and difficult to measure. The importance of NTFPs is still under-represented in sustainable forest management planning.

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19.1 Introduction

Amazonian floodplain trees are used for a variety of purposes (i.e. Le Cointe 1922; Phillips et al. 1994; Parolin 2000a; 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.

In general, floodplain inhabitants have preserved an intimate knowledge of the floodplain environment and its resources (e.g., Hiraoka 1992; Padoch 1988; Junk et al. 2000a) such that the management of crops and trees is adapted to the environment (Ohly 2000b; De Jong 2001). Most information about the use of forest resources in Ecuador, Peru, Colombia, Bolivia, and the Guyanas originates from the Amerindian population. However, the majority of floodplain inhabitants in Brazilian Amazonia are descendants of colonists and their use of forest resources may differ substantially from that of the Amerindian population.

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

19.2 Non-Timber Forest Products

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

In várzea forests, quantitative inventories of the ratio species pool/useful species range from 48% to 87% of all tree species. In a floristic inventory comprising 7.5 ha of várzea forests, Pinedo-Vásquez et al. (1990) reported that floodplain inhabitants in northern Peru use 60.1% of all tree species present. In a quantitative ethnobotanical investigation of terra firme and floodplain (várzea) forests along the 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 useful to the inhabitants. Contrary to the findings of Grimes et al. (1994), the authors noted that floodplain forests are more useful than other forest types, mostly due to their importance as sources of construction materials and food. About 80% of forest plant products were of subsistence value (not sold) for floodplain inhabitants, whereas about 20% were of commercial value. The authors also concluded that forests, especially those of the floodplain, are endangered through intense deforestation and overexploitation.

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

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

We compiled information on the use of 186 common várzea tree species (*sensu* Wittmann et al. 2006a, Table 19.1) within the Amazon basin, based on information from: (a) herbaria (mainly the Instituto Nacional de Pesquisas da Amazonia (INPA), Manaus, Brazil; Missouri Botanical Garden (MBG), USA; New York Botanical Garden (NYBG), USA, Royal Botanical Gardens, Kew, Great Britain) and (b) the literature (i.e., Phillips and Gentry 1993; Phillips et al. 1994; Kvist et al. 2001; Worbes et al. (2001); Schöngart (2003); Reyes-García et al. 2006), or more specialized literature about the chemical constituents of plants (see Table 19.3). Only those trees usually cut as a whole for use (roundwood, house and boat construction, floating houses, carpentry, panelling, floors, sleepers, instrument shafts, plywood, etc.) were considered as timber species. Other uses were considered to provide NTFPs (medical uses, edible fruits, fish baits, fishing and hunting poisons, palm hearts, firewood, manufacture of oars, fishing rods, arrows and bows, resins, fuels, fragrances, pigments, phytocosmetics, hedges, tying, braiding, roof construction, vessels, etc.). The results indicated that 135 tree species (72.6%) are useful to floodplain inhabitants and/or extractors (Table 19.2). This amount is well within the range of data from the previously described ethnobotanical inventories. 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, leishmaniosis, 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 phytomedical extracts from várzea tree species are listed in Table 19.3.

Thirty-one species provide edible fruits (Table 19.1), most which are rarely sold 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

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)

Family	Species	No known use	NTFPs						Timber
			Phytomedical	Edible fruits	Fish bait	Ornamental tree	Handicrafts	Other	
Anacardiaceae	*Spondias lutea* L.		x	x				x	x
Annonaceae	*Annona hypoglauca* Mart.			x					
	Annona tenuipes R.E.Fries								x
	Duguetia quitarensis Benth.							x	
	Duguetia spixiana Mart.								x
	Guatteria inundata Mart.							x	
	Oxandra riedeliana R.E.Fries								x
	Unonopsis floribunda Diels	x							
	Unonopsis guatterioides (A.DC.) R.E.Fries		x						x
	Xylopia calophylla R.E.Fries							x	x
Apocynaceae	*Aspidosperma rigidum* Rusby		x					x	x
	Himatanthus sucuuba (Spruce ex Müll. Arg.) Woodson		x						

(continued)

Table 19.1 (continued)

Family	Species	No known use	NTFPs						Timber
			Phytomedical	Edible fruits	Fish bait	Ornamental tree	Handicrafts	Other	
	Malouetia tamaquarina (Aubl.) A.DC.		x				x		
	Tabernaemontana markgrafiana J.F.Macbr.		x						
	Tabernaemontana siphilitica (L.f.) Leeuwenb.		x						
Aquifoliaceae	*Ilex inundata* Poepp. ex Reissek				x				
Arecaceae	*Astrocaryum jauari* Mart.				x			x	
	Attalea phalerata Mart. ex Spreng.						x	x	
	Bactris brongniartii Mart.			x					
	Bactris concinna Mart.			x					
	Bactris riparia Mart.	x							
	Euterpe precatoria Mart.			x		x		x	x
	Mauritia flexuosa L.f.			x				x	
	Oenocarpus bataua Mart.			x				x	
Bignoniaceae	*Crescentia amazonica* Ducke						x	x	
	Crescentia cujete L.		x			x	x	x	

	Tabebuia barbata (E.Mey) Sandwith		x					x
	Tabebuia serratifolia (Vahl) G.Nicholson		x			x		x
Boraginaceae	*Cordia nodosa* Lam.	x						
Brassicaceae	*Crataeva benthamii* Eichler				x			
Burseraceae	*Protium strumosum* Daly	x						
Caryocaraceae	*Caryocar microcarpum* Ducke			x			x	x
Chrysobalanaceae	*Couepia chrysocalyx* (Poepp.) Benth. ex Hook f.	x						
	Couepia paraensis (Mart. and Zucc.) Hook f.			x				
	Licania apetala (E.Mey) Fritsch						x	x
	Licania brittoniana Fritsch	x						
	Licania heteromorpha Benth.		x	x			x	
	Licania longistyla (Hook f.) Fritsch			x				
	Parinari excelsa Sabine			x				x
	Tapura juruana (Ule) Rizzini	x						

(continued)

Table 19.1 (continued)

Family	Species	No known use	NTFPs						Timber
			Phytomedical	Edible fruits	Fish bait	Ornamental tree	Handicrafts	Other	
Clusiaceae	*Calophyllum brasiliense* Camb.		x						x
	Caraipa punctulata Ducke							x	x
	Clusia panapanari (Aubl.) Choisy	x							
	Garcinia brasiliensis Mart.		x	x					x
	Garcinia madruno (Kunth) Hammel			x					
	Tovomita umbellata Benth.	x							
	Vismia baccifera (L.) Triana and Planch.							x	x
	Vismia macrophylla Kunth		x						
Combretaceae	*Buchenavia oxycarpa* (Mart.) Eichler								x
	Terminalia dichotoma G.Mey.								x
Elaeocarpaceae	*Sloanea floribunda* Spruce ex Benth.	x							
	Sloanea terniflora (Sessé and Moc. ex DC.) Standl.				x				x
Erythroxylaceae	*Erythroxylum capplerianum* Peyr.	x							

	Erythroxylum tucuriense Plowman	x					
Euphorbiaceae	*Alchornea castaneifolia* (Humb. and Bonpl.) A.Juss.		x				
	Alchornea discolor Poepp.			x		x	
	Discocarpus brasiliensis Klotzsch	x					
	Hevea brasiliensis (Willd. ex A.Juss.) Müll.Arg.					x	x
	Hevea pauciflora (Spruce ex Benth.) Müll.Arg.					x	
	Hevea spruceana (Benth.) Müll.Arg.				x	x	
	Hura crepitans L.					x	x
	Mabea nitida Spruce ex Benth.			x			
	Piranhea trifoliata Baill.						x
	Sapium glandulosum (L.) Morong				x	x	
Lauraceae	*Aniba affinis* (Meisn.) Mez.	x					
	Aniba hostmanniana (Nees) Mez.	x					

(continued)

Table 19.1 (continued)

Family	Species	No known use	NTFPs						Timber
			Phytomedical	Edible fruits	Fish bait	Ornamental tree	Handicrafts	Other	
	Aniba megaphylla Mez.	x							
	Aniba riparia (Nees) Mez.		x						x
	Endlicheria anomala (Nees) Mez.								x
	Endlicheria formosa A.C.Sm.								x
	Licaria armeniaca (Nees) Kosterm.								x
	Nectandra amazonum Nees								x
	Nectandra hihua (Ruiz. and Pav.) Rohwer	x							
	Ocotea aciphylla (Nees) Mez.								x
	Ocotea cymbarum Kunth		x					x	x
Lecythidaceae	*Couroupita subsessilis* Pilg.		x			x		x	x
	Eschweilera albiflora (DC.) Diers								x
	Eschweilera ovalifolia (DC.) Nied								x

	Eschweilera parviflora Mart. ex DC.					x	
	Gustavia augusta L.		x				
	Gustavia poeppigiana O.Berg	x					
	Lecythis pisonis Camb.			x		x	x
Fabaceae: Caesalpinioideae	*Acosmium nitens* (Vogel) Yakovlev						x
	Campsiandra comosa Benth.			x			
	Cassia leiandra Benth.		x	x	x		
	Copaifera officinalis (Jacq.) L.		x			x	x
	Crudia amazonica Spruce ex Benth.	x					
	Cynometra bauhinifolia Benth.						x
	Macrolobium acaciifolium (Benth.) Benth.						x
	Macrolobium bifolium (Aubl.) Pers.						x
	Schizolobium amazonicum Huber ex Ducke						x

(continued)

Table 19.1 (continued)

Family	Species	No known use	NTFPs						Timber
			Phytomedical	Edible fruits	Fish bait	Ornamental tree	Handicrafts	Other	
	Senna bacillaris (L.f.) H.S.Irwin and Barneby		x	x					
	Senna reticulata (Willd.) H.S.Irwin and Barneby	x							
	Tachigali venusta Dwyer	x							
Fabaceae: Mimosoideae	*Acacia loretensis* J.F.Macbr.								x
	Albizia subdimidiata (Splitg.) Barn. and Grimes	x							
	Hydrochorea corymbosa (Rich.)Barn. and Grimes	x							
	Inga cinnamonea Spruce ex Benth.			x					
	Inga disticha Benth.	x							
	Inga obidensis Ducke	x							
	Inga pilosula (Rich.) J.F.Macbr.			x					
	Inga punctata Willd.			x					
	Inga splendens Willd.	x							
	Pseudopiptadenia suaveolens (Miq.) Grimes								x

	Stryphnodendron guianense (Aubl.) Benth.	x							
	Zygia cataractae (Kunth) L.Rico			x					
	Zygia latifolia (L.) Fawcett and Rendle	x							
Fabaceae: Papillionoideae	*Clitoria amazonum* Mart. ex Benth.	x							
	Erythrina fusca Lour.		x						x
	Etaballia dubia (Kunth) Rudd.								x
	Lecointea amazonica Ducke							x	x
	Ormosia macrocalyx Ducke				x		x		
	Paramachaerium ormosioides (Ducke) Ducke								x
	Platymiscium ulei Harms								x
	Pterocarpus amazonum (Mart. ex Benth.) Ams.					x			x
	Vatairea guianensis Aubl.		x						x

(continued)

Table 19.1 (continued)

Family	Species	No known use	NTFPs						Timber
			Phytomedical	Edible fruits	Fish bait	Ornamental tree	Handicrafts	Other	
Malpighiaceae	*Byrsonima japurensis* A.Juss.								x
	Glandonia macrocarpa Griseb.	x							
Malvaceae	*Apeiba glabra* Aubl.								x
	Ceiba pentandra (L.) Gaertn.							x	x
	Guazuma ulmifolia Lam.		x						x
	Herrania mariae (Mart.) Decne ex Goudot			x					
	Luehea cymulosa Spruce ex Benth.								x
	Pachira insignis (Sw.) Sw. ex Savigny			x					x
	Pseudobombax munguba (Mart. and Zucc.) Dug.						x	x	x
	Sterculia apetala (Jacq.) H.Karst			x		x			x
	Theobroma cacau L.		x	x					
Melastomataceae	*Mouriri acutiflora* Naudin								x
	Mouriri grandiflora DC.								x
Meliaceae	*Cedrela odorata* L.		x				x		x
	Guarea guidonia (L.) Sleumer		x						x

	Trichilia lecointei Ducke						x
Moraceae	*Batocarpus amazonicus* (Ducke) Fosberg						x
	Ficus anthelmintica Mart.		x				x
	Ficus amazonica (Miq.) Miq.	x					
	Ficus casapiensis Dugand	x					
	Ficus guianensis Desv. ex Ham.				x		
	Ficus matthewsii Standl.	x					
	Helicostylis scabra (J.F.Macbr.) C.C.Berg			x			
	Maclura tinctoria (L.) D.Don. ex Steud.		x	x		x	x
	Maquira calophylla (Poepp. and Endl.) C.C.Berg		x				
	Maquira coriacea (H.Karst) C.C.Berg		x			x	x
	Sorocea duckei W.C.Burger	x					
Myristicaceae	*Virola calophylla* (Spruce) Warb.		x				x

(continued)

Table 19.1 (continued)

Family	Species	No known use	NTFPs						Timber
			Phytomedical	Edible fruits	Fish bait	Ornamental tree	Handicrafts	Other	
	Virola mollissima (Poepp. Ex A.DC.) Warb.	x							
	Virola surinamensis (Roll. Ex Rottb.) Warb.		x					x	x
Myrsinaceae	*Cybianthus spicatus* (Kunth) G.Agostini	x							
Myrtaceae	*Calypthrantes multiflora* O.Berg			x					
	Eugenia inundata DC.	x							
	Eugenia ochrophloea Diels	x							
	Myrciaria dubia (Kunth) Mc Vaugh			x					
	Psidium acutangulum DC.			x					
Nyctaginaceae	*Neea aeuginosa* Standl.	x							
	Neea spruceana Heimerl				x				
Ochnaceae	*Quiina rhytidopus* Tul.	x							
Olacaceae	*Heisteria acuminata* (Humb. and Bonpl.) Engl.		x						x
	Minquartia guianensis Aubl.								x
Polygonaceae	*Symmeria paniculata* Benth.				x	x			

	Triplaris dugandii Brandbyge	x					
	Triplaris surinamensis Cham.						x
Rubiaceae	*Alibertia edulis* (Rich.) A.Rich ex DC.			x		x	
	Bothriospora corymbosa (Benth.) Hook.f.	x					
	Calycophyllum spruceanum (Benth.) Hook.f. ex K.Schum.		x		x	x	x
	Duroia duckei Huber	x					
	Genipa americana L.		x			x	x
Rutaceae	*Zanthoxylum compactum* (Huber ex Albuq.) P.G.Waterman	x					
Salicaceae	*Banara guianensis* Aubl.	x					
	Casearia aculeata Jacq.	x					
	Homalium guianense (Aubl.) Oken	x					
	Laetia corymbulosa Spruce ex Benth.		x				x
	Salix martiana Leyb.		x			x	
	Xylosma benthamii (Tul.) Triana and Planch.	x					

(continued)

Table 19.1 (continued)

Family	Species	No known use	NTFPs						Timber
			Phytomedical	Edible fruits	Fish bait	Ornamental tree	Handicrafts	Other	
Sapotaceae	*Chrysophyllum argenteum* Jacq.								x
	Micropholis egensis (A.DC.) Pierre	x							
	Pouteria elegans (A.DC.) Baehni	x							
	Pouteria glomerata (Pohl ex Miq.) Radlk.	x							
	Pouteria procera (Mart.) T.D.Penn.			x	x				x
Simaroubaceae	*Simaba multiflora* A.Juss.		x						
Theophrastaceae	*Clavija lancifolia* Desf.	x							
Urticaceae	*Cecropia latiloba* Miq.	x							
	Cecropia membranacea Trécul	x							
	Coussapoa nitida Miq.		x						
	Pourouma guianensis Aubl.		x						
Verbenaceae	*Vitex cymosa* Bertero ex Spreng.		x		x	x			x
Violaceae	*Leonia glycycarpa* Ruiz and Pav.			x					
Vochysiaceae	*Vochysia guianensis* Aubl.								x

Table 19.2 Use categories of the 186 investigated tree species from the Amazonian várzea (for category definition, see text). 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)

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

found in non-flooded (sometimes pan-tropical) environments but that are cultivated by floodplain inhabitants in home gardens (Gutjahr 1996; Junk et al. 2000a). These tree species, e.g. *Mangifera indica* L. (mango), *Eugenia malaccensis* L. (jambo), *Artocarpus altilis* (Parkinson) Fosberg (breadfruit), *Cocos nuccifera* L. (coconut),

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)

	Phyto-medical use									
Species	1	2	3	4	5	6	7	8	Other	Source
Alchornea castaneifolia (Humb. and Bonpl.) A. Juss.	x			x					Anti-viral, analgesic	H; Dunstan et al. (1997);Barros (2004); Hiruma-Lima et al. (2006)
Aniba riparia (Nees) Mez.									Anti-depressive, Anxiolytic	H; Sousa et al. (2004)
Aspidosperma rigidum Rusby			x				x			H
Calophyllum brasiliense Cambess.	x								Anti-diabetes	H; Pretto et al. (2004)
Calycophyllum spruceanum (Benth.) Hook f.	x			x						H
Cassia leiandra Benth.				x						H
Cedrela odorata L.			x							H; Martins et al. (2003)
Copaifera officinalis (Jacq.) L.		x					x		Antiseptic	H; Lima et al. (2003)
Couroupita subsessilis Pilg.				x					Antibiotic	H
Coussapoa nitida Miq.				x						Herforth et al. (2003)
Crescentia cujete L.			x			x	x			H
Erythrina fusca Lour.					x	x		x	Anti-microbial	Payne (1991)
Ficus anthelmintica Rich. ex DC.					x					H
Garcinia brasiliensis Mart.	x	x		x				x		H
Genipa americana L.			x				x		Antibiotic	Gonçalves et al. (2005)
Guarea guidonia (L.) Sleumer			x		x	x				Oga et al. (1981)
Guazuma ulmifolia Lam.		x							Antibiotic	Camporese et al. (2003);Seigler (2005)
Gustavia augusta L.	x								Anti-leishmaniosis	De Souza et al. (2001)
Heisteria acuminata (Humb. & Bonpl.) Engl.	x									Kraus et al. (1998)
Himatanthus sucuuba (Spruce ex Müll. Arg.) Wood.	x		x		x				Analgesic	H; De Miranda et al. (2000)
Laetia corymbulosa Spruce ex Benth.		x								Beutler et al. (2000)
Licania heteromorpha Benth.									Anti-microbial	Braca et al. (2000)

Maclura tinctoria (L.) D. Don ex Steud.				x					Anti-viral	El-Sohly et al. (1999); Groweiss et al. (2000)
Malouetia tamaquarina (Aubl.) A. DC.		x						x		Suffredini et al. (2002)
Maquira calophylla (Poepp. and Endl.) C.C. Berg		x								Rovinski et al. (1987)
Maquira coriacea (H. Karst) C.C. Berg									Anti-plasmodial	Mitaine-Offer et al. (2001)
Ocotea cymbarum Kunth	x					x				H
Pourouma guianensis Aubl.									Anti-leishmaniosis	H; Torres-Santos et al. (2004)
Salix martiana Leyb.	x									H
Senna bacillaris (L. f.)H. S. Irwin & Barneby						x				Mabberley (1997)
Simaba multiflora A. Juss.		x							Anti-malarial	Moretti et al. (1986); Cabral et al. (1993))
Spondias lutea L.	x									Kvist et al. (2001)
Tabebuia barbata (E. Mey.) Sandwith		x								De Saizarbitoria et al. (1997)
Tabebuia serratifolia (Vahl) G. Nicholson		x	x						Anti-Leishmaniosis	Duke and Vázquez (1994)
Tabernaemontana markgrafiana J. F. Macbr.			x	x					Disinfectant	Nielsen et al. (1994)
Tabernaemontana siphillitica (L.f.) Leeuwenb.	x		x							H
Theobroma cacao L.					x				Stimulant, antiseptic	Leung (1980)
Unonopsis floribunda Diels	x								Diarrhea	H
Vatairea guianensis Aubl.									Anti-mycotic	H
Virola calophylla (Spruce) Warb.								x		H
Virola surinamensis (Rol. ex Rottb.) Warb.									Anti-malarial	Lopes et al. (1999)
Vismia macrophylla Kunth	x	x								H; Lopez et al. (2001); Husseein et al. (2003)
Vitex cymosa Bert. ex Spreng.									Analgesic	H

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

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

One modern use of tree species that is rarely mentioned in literature is as ornamental trees. These are of increasing importance because municipalities are interested in improving the quality of life of city inhabitants by cultivating trees that reduce solar radiation, improve air quality, and are visually attractive, i.e., by producing large and colorful flowers. Ornamental trees are, optimally, fast-growing species that are resistant to stressful conditions, such as seasonal drought, soil compaction, and elevated anthropogenic gas imissions, while negative properties, such as the development of large buttresses, massive leaf shedding, and the production of large fruits, are not desired. We identified 13 central Amazonian várzea tree species that are used as ornamental trees in Brazilian cities (Table 19.1). Some of these tree species, including *Vitex cymosa, Ficus guianensis* and *Ceiba pentandra*, are widely distributed throughout the neotropics, while others, e.g., *Cassia leiandra* and *Pterocarpus amazonum*, have restricted distribution patterns in the Amazonian várzea. Fast-growing and light-demanding várzea species, such as *Pseudobombax munguba* and *Triplaris surinamensis*, were recently planted along the devastated banks of small rivers (igarapés) in the city of Manaus (Secretaria Municipal do Meio Ambiente (SEMMA), Manaus; Oliveira Wittmann, A., 2003, personal communication).

19.3 Timber Products

Although the area covered by floodplain forests is smaller than the accounted for by Amazonian terra firme, about 70–75% of the wood exploited in Amazonia 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 350,000 m^3 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. 2001d; 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 cities Itacoatiara, Manaus, and Tefé. While deforestation is concentrated around settlements along the main river channels, timber exploitation occurs also in more isolated areas, because roundwood is transported to the sawmills by rafting during high-water periods, when the cost of transport is less than that incurred by trucks hauling timber from the uplands (Higuchi et al. 1994; Barros and Uhl 1999; Albernaz and Ayres 1999). The overexploitation of comparatively few commercially used tree species in some regions along the Solimões, Madeira, Purús, and Japurá Rivers already has led to their substitution by alternative species on the local timber markets, such as the substitution of the high-density wood species *Cedrela odorata* and *Platymiscium ulei* by *Ocotea cymbarum*, *Calycophyllum spruceanum*, and *Piranhea trifoliata*, and the substitution of the low-density wood species *Ceiba pentandra* and *Virola* spp. by *Sterculia apetala*, *Ficus anthelmintica*, and *Couroupita subsessilis* (Ayres 1993; Worbes et al. 2001; Schöngart 2003).

Specific information about the uses of timber species by floodplain inhabitants is scarce, but several authors reported that the most important use of floodplain timber is house and boat construction (Phillips et al. 1994; Kvist et al. 2001; Luna 2004). Using literature data describing the mechanical characteristics of wood, Worbes et al. (2001) and Schöngart (2003) investigated the actual and potential use of timber trees originating from Amazonian floodplains. The investigation about the use of 186 common central Amazonian várzea tree species indicate that less tree species are used for timber (78 species, 41.9%) than for NTFPs (Table 19.2, but note that the large majority of timber species also provide NTFPs). We separated the fate of timber into nine categories with respect to its use: home construction, heavy construction and sleepers, boat and canoe construction (including roundwood for houseboats), carpentry, furniture, flooring and panels, plywood, tools

Table 19.4 Species occurrence, wood-specific gravity (SG) ranges (if available; no range is indicated from poorly inventoried species), and actual uses of 78 timber tree species from the Amazonian várzea. Only use categories involving tree cutting as a whole are listed. LV = low várzea (mean flood height >3.0 m); HV = high várzea (mean flood height <3.0 m). ISDM = Information provided by the Forest Management Programme of the Institute of Sustainable Development Research Mamirauá, Tefé, Brazil (SG ranges were obtained from Brown 1997; Fearnside 1997; Worbes et al. 2001; Ter Steege 2000; Schöngart 2003; Wittmann et al. 2006b; Stadtler 2007)

	Occurrence		WSG	Use category									
Species	LV	HV	(g cm^{-3})	1	2	3	4	5	6	7	8	9	Source
Acacia loretensis J.F. Macbr.	x		–	x								x	ISDM
Acosmium nitens (Vogel) Yakovlev	x		0.72–0.76	x	x		x				x		ISDM; Worbes et al. (2001)
Aniba riparia (Nees) Mez.		x	0.39–0.46	x								x	ISDM
Annona tenuipes R.E.F ries	x		–	x								x	ISDM
Apeiba glabra Aubl.		x	–	x	x						x		ISDM; Phillips et al. (1994)
Aspidosperma rigidum Rusby		x	–							x			ISDM
Batocarpus amazonicus (Ducke) Fosberg		x	0.71–0.77	x				x					Phillips et al. (1994); Kvist et al. (2001)
Buchenavia oxycarpa (Mart.) Eichler		x	0.72–0.77	x	x		x		x			x	ISDM
Byrsonima japurensis A. Juss.	x	x	–	x									ISDM
Calophyllum brasiliense Camb.		x	0.51–0.68	x	x	x		x	x	x			ISDM; Silva (1977); Phillips et al. (1994); Kvist et al. (2001); Santos et al. (2004)
Calycophyllum spruceanum (Benth.) Hook f.		x	0.74–0.81	x			x	x	x	x			ISDM; Kvist et al. (2001); Worbes et al. (2001)
Caraipa punctulata Ducke		x	–	x									ISDM
Caryocar microcarpum Ducke		x	0.58–0.64	x	x				x		x		ISDM; Silva (1977); Worbes et al. (2001); Kvist et al. (2001)
Cedrela odorata L.		x	0.48–0.60	x	x	x		x	x				ISDM; Parotta et al. (1995); Silva (1977)
Ceiba pentandra (L.) Gaertn.		x	0.21–0.34		x	x					x		ISDM; Parotta et al. (1995); Kvist et al. (2001)
Chrysophyllum argenteum Jacq.		x	0.70–0.75	x						x			ISDM; Kvist et al. (2001)
Copaifera officinalis (Jacq.) L.		x	0.59			x		x			x		ISDM
Couroupita subsessilis Pilg.		x	0.45–0.55			x		x	x		x		ISDM
Cynometra bauhinifolia Benth.	x		0.78–0.82	x									ISDM

(continued)

Table 19.4 (continued)

Species	Occurrence		WSG	Use category									Source
	LV	HV	(g cm^{-3})	1	2	3	4	5	6	7	8	9	
Duguetia spixiana Mart.	x		–	x								x	ISDM; Phillips et al. (1994); Kvist et al. (2001)
Endlicheria anomala (Nees) Mez.	x	x	0.48	x				x					ISDM
Endlicheria formosa A.C. Sm.		x	–	x									Phillips et al. (1994); Luna (2004)
Erythrina fusca Lour.		x	0.31–0.33		x	x							ISDM
Eschweilera albiflora (DC.) Diers	x	x	0.66–0.83				x						ISDM
Eschweilera ovalifolia (DC.) Nied	x		–	x	x								ISDM
Etaballia dubia (Kunth) Rudd.		x	0.62–0.66	x									ISDM
Euterpe precatoria Mart.			–	x									ISDM; Henderson et al. (1995); Kvist et al. (2001)
Ficus anthelmintica Rich. ex DC.	x		0.35–0.38								x		ISDM; Phillips et al. (1994)
Garcinia brasiliensis Mart.		x	0.58–0.64	x									ISDM
Genipa americana L.		x	0.57–0.66	x		x	x	x	x	x		x	ISDM; Kvist et al. (2001)
Guarea guidonia (L.) Sleumer		x	0.53	x			x	x					ISDM; Phillips et al. (1994)
Guazuma ulmifolia Lam.		x	0.49–0.52			x							ISDM
Heisteria acuminata (Humb. & Bonpl.) Engl.		x	–	x									ISDM; Phillips et al. (1994)
Hevea brasiliensis Müll. Arg.		x	0.52–0.64	x		x		x					Worbes et al. (2001)
Hura crepitans L.		x	0.36–0.42	x	x	x		x	x		x		ISDM; Phillips et al. (1994);Albernaz and Ayres (1999); Kvist et al. (2001)
Laetia corymbulosa Spruce ex Benth.	x		0.61–0.67	x									Kvist et al. (2001)
Lecointea amazonica Ducke		x	0.97–1.03	x			x			x			ISDM; Kvist et al. (2001)
Lecythis pisonis Camb.		x	0.84	x			x			x			ISDM
Licania apetala (E. Mey.) Fritsch	x		0.64–0.78	x									ISDM; Kvist et al. (2001)
Licaria armeniaca (Nees) Kosterm.	x		0.44–0.51	x	x								ISDM; Phillips et al. (1994); Kvist et al. (2001)
Luehea cymulosa Spruce ex Benth.	x		0.38–0.48		x	x					x		ISDM; Worbes et al. (2001)
Maclura tinctoria (L.) D. Don. ex Steud.	x		0.69–0.73	x	x								ISDM

Macrolobium acaciifolium (Benth.) Benth.	x		0.43–0.49	x		x		x				ISDM; Worbes (1997); Kvist et al. (2001); Santos et al. (2004)
Macrolobium bifolium (Aubl.) Pers.	x	x	0.46	x							x	ISDM
Maquira coriacea (H. Karst) C.C. Berg		x	0.45–0.49	x		x		x		x		ISDM; Kvist et al. (2001), Worbes et al. (2001)
Minquartia guianensis Aubl.		x	0.76–0.88	x			x					ISDM; Silva (1977); Phillips et al. (1994); Kvist et al. (2001); Santos et al. (2004)
Mouriri acutiflora Naudin		x	0.77–0.82				x					ISDM
Mouriri grandiflora DC.		x	–	x								Kvist et al. (2001)
Nectandra amazonum Nees	x		0.38–0.47	x								ISDM
Ocotea aciphylla (Nees) Mez.		x	0.58–0.63	x								ISDM; Marques (2001)
Ocotea cymbarum Kunth		x	0.58–0.62	x	x	x		x	x	x		ISDM; Albernaz and Ayres (1999); Worbes et al. (2001)
Oxandra riedeliana R. E. Fries	x		0.47–0.51	x								ISDM; Phillips et al. (1994)
Pachira insignis (Sw.) Sw. ex Savigny		x	0.43–0.47							x		Phillips et al. (1994)
Paramachaerium ormosioides (Ducke) Ducke		x	0.37–0.42	x				x				ISDM
Parinari excelsa Sabine		x	0.64–0.68	x	x		x					ISDM; Worbes et al. (2001)
Piranhea trifoliata Baill.	x		0.86–0.94	x		x	x					ISDM; Worbes et al. (1992)
Platymiscium ulei Harms		x	0.73–0.77	x	x		x	x	x			ISDM; Silva (1977); Worbes et al. (2001)
Pouteria procera (Mart.) T. D. Penn.		x	0.65–0.73	x								ISDM; Phillips et al. (1994); Kvist et al. (2001)
Pseudobombax munguba (Mart. & Zucc.) Dug.	x		0.21–0.29			x			x			ISDM
Pseudopiptadenia suaveolens (Miq.) J.W. Gr.		x	0.59	x						x		ISDM; Phillips et al. (1994)
Pterocarpus amazonum (Mart. ex Benth.) Amsh.	x		0.33–0.38	x	x							Phillips et al. (1994); Santos et al. (2004)

(continued)

Table 19.4 (continued)

Species	Occurrence		WSG	Use category									Source
	LV	HV	(g cm^{-3})	1	2	3	4	5	6	7	8	9	
Schizolobium amazonicum Huber ex Ducke		x	0.58–0.64	x							x		ISDM; Brienza-Junior et al. (1991)
Sloanea terniflora (Sessé & Moc. .) Standl.	x	x	0.63–0.71	x		x							ISDM; Phillips et al. (1994)
Spondias lutea L.		x	0.31–0.41			x		x			x		Worbes et al. (2001); Santos et al. (2004)
Sterculia apetala (Jacq.) H. Karst		x	0.33–0.36	x	x	x		x			x		ISDM; Worbes et al. (2001)
Tabebuia barbata (E. Mey) Sandwith	x		0.65–0.79	x			x						ISDM; Albernaz and Ayres (1999)
Tabebuia serratifolia (Vahl) G. Nicholson		x	0.87–1.01	x	x	x	x		x				ISDM
Terminalia dichotoma G. Mey.	x		0.64–0.68	x	x								ISDM
Trichilia lecointei Ducke		x	0.70–0.88	x			x						ISDM
Triplaris surinamensis Cham.	x		0.51–0.63	x		x		x					Worbes et al. (2001)
Unonopsis guatterioides (A. DC.) R.E. Fries		x	0.42–0.48								x		ISDM; Worbes et al. (2001)
Vatairea guianensis Aubl.	x		0.70–0.75	x				x	x				ISDM; Worbes et al. (2001)
Virola calophylla (Spruce) Warb.		x	0.48–0.64	x									ISDM; Phillips et al. (1994)
Virola surinamensis (Rol. ex Rottb.) Warb.		x	0.37–0.42	x		x		x	x		x		ISDM; Phillips et al. (1994); Anderson et al. (1999); Worbes et al. (2001); Santos et al. (2004)
Vismia baccifera (L.) Triana and Planch.	x		0.54–0.60	x								x	ISDM
Vitex cymosa Bert. ex Spreng.	x		0.56–0.59	x									ISDM
Vochysia guianensis Aubl.		x	0.40–0.65	x									ISDM
Xylopia calophylla R.E. Fries		x	0.33–0.37						x			x	ISDM; Phillips et al. (1994)

(e.g., instrument shafts), and fences (Table 19.2). The results showed that most timber trees are used for multiple purposes (Table 19.4). Quantitatively, the category containing the most species was house construction (63 species), followed by carpentry (22 species), furniture (21 species), and boat, houseboat, and canoe construction (20 species, e.g., *Apeiba glabra*, *Buchenavia oxycarpa*, and *Hura crepitans*). Eighteen tree species are commercially harvested for plywood (among the most important: *Hura crepitans*, *Ceiba pentandra*, *Ocotea cymbarum*, *Couroupita subsessilis*, *Schizolobium amazonicum*, *Sterculia apetala*, and *Maquira coriacea,* Table 19.4), some of them representing species with no or only little commercial values for local inhabitants. Such species include *Ficus anthelmintica* and *Pseudopiptadenia suaveolens* (but note that the former provides NTFPs, Table 19.3).

During the last several years, the price of central Amazonian várzea timber has consistently increased, from US\$7.90–11.40 m^{-3} (low-density wood) and US\$15.20 m^{-3} (high-density wood) in the year 2003 to approximately US\$17.50 m^{-3} and 31.00 m^{-3} in the year 2007 (Forest Managament Programme Mamirauá, Schöngart et al. 2010). Based on the normative regulations established by the IBAMA (minimum logging diameter of 45 cm, cutting cycle of 25 years, and a maximum yield of 5 trees ha^{-1}), the NPV from selectively logged várzea timber thus actually ranges between US\$13.80 and 51.36 ha^{-1} year^{-1}. Unfortunately, we have no comparable data for the NPV of NTFPs.

19.4 Conclusions

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.

Chapter 20
Traditional Timber Harvesting in the Central Amazonian Floodplains

Jochen Schöngart and Helder Lima de Queiroz

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20.1 Introduction

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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cycle and reducing the energy of water and erosion. Moreover, floodplain forests are habitats for highly adapted plant and animal species, many of them endemic to the várzea. They also represent important sinks and sources for biogeochemical cycles (Piedade et al. 2001; Schöngart et al. 2010) and are an important food source for many fish species, which in turn are the primary protein base for the local human population (Junk et al. 1997, 2000a). In this context, sustainable management of tropical forests offers promise to safeguard the socio-ecologically important multiple functions and services of forest ecosystems and to guarantee the use of natural resources for the growing population in Amazonia. In this chapter the traditional timber extraction in the Amazonian várzea and the socio-economic improvements it provides to the local population are described and discussed as an example of community forest management as practiced in the Mamirauá Sustainable Development Reserve (MSDR) (Queiroz and Peralta 2010).

20.2 Traditional Commercial Timber Harvesting in Amazonian Floodplain Forests

Parallel to the decline of timber stocks in Southeast Asia and within Brazil's southern region and coastal rainforests (*Mata Atlânica*), the Amazon basin with its immense forest resources has acquired increasing importance as source of tropical timber (Veríssimo et al. 1992). Prior to the 1980s, almost all logging was in the form of "river scratching" in floodplain forests adjacent to the major rivers, mainly in eastern Amazonia. The rivers served as easy access for the loggers and transport route for timber for more than three centuries (Anderson et al. 1999; Fortini et al. 2006). Many tree species from floodplain forests were and still are utilized for non-timber products, such as resins, oils, palm hearts, edible fruits, textile fibres, tannins, kapok, and medicinal purposes (Kvist et al. 2001; Wittmann and Oliveira Wittmann 2010). With the beginning of the rubber boom, in the mid-nineteenth century, logging increased in floodplain forests. Extracted fuelwood provided an energy supply both for steamboats and for the vulcanization of latex (*Hevea brasiliensis*), thereby sustaining the growing population of Manaus (Ohly 2000b; Parolin 2000a).

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

In the western Amazon basin of Brazil and Peru, access to terra firme forests is 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 g cm^{-3}), and high-density tree species (*madeira pesada*), with wood densities above 0.60 g cm^{-3} (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 2010). 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. 2010). 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 ha^{-1} 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 ha^{-1} 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 ha^{-1} 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 ha of timber species (>10 cm), with a basal area of 2.6–10.0 m^2 ha^{-1} and a volume of 59–240 m^3 ha^{-1}. 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 m^3 ha^{-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

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

Timber species with diameter >45 cm	Middle Solimões River	Upper Juruá River	Middle Juruá River	Madeira River	Purus River
Forest inventory (ha)	6	8	5	6	2
High-density tree species					
Manilkara spp.	0.9	2.4	1.2	0.6	2.0
Pouteria sp.	1.6	2.3	1.5	0.7	1.4
Calycophyllum spruceanum	1.8	1.3	0.6	1.4	0.2
Calophyllum brasiliense	0.6	0.1	0.2		
Copaifera sp.	0.3	0.1	0.6		0.4
Piranhea trifoliata	0.5			0.8	1.3
Vatairea guianensis	0.6			0.7	0.4
Carapa guianensis		0.1	0.4		0.2
Guarea spp.	0.7				
Ocotea cymbarum			0.1		
Subtotal	7.0	6.3	4.6	4.2	5.9
	(57%)	(51%)	(43%)	(46%)	(58%)
Low-density tree species					
Hura crepitans	2.0	1.6	2.3	0.8	1.5
Virola spp.	0.9	1.7	1.3	1.7	0.8
Maquira coriacea	2.1		0.9	1.0	1.0
Ceiba pentandra	0.2	1.0	0.5	0.3	0.6
Ficus insipida		0.8	0.2	0.7	0.2
Macrolobium acaciifolium		1.0	0.2		0.2
Couroupita subsessilis			0.7		
Sterculia elata				0.4	
Subtotal	5.2	5.1	6.1	4.9	4.3
	(43%)	(49%)	(57%)	(54%)	(42%)
Total	**12.2**	**12.4**	**10.7**	**9.1**	**10.2**

plywood and veneer industries (Lima et al. 2005). The low-density species *H. crepitans*, *M. coriacea*, *C. pentandra*, and *Virola* spp. together with the high-density species *Manilkara* sp., *C. odorata*, *O. cymbarum*, *C. spruceanum*, *Calophyllum brasiliense*, and *Copaifera* sp. comprise 70–90% of the total timber exploitation (Table 20.2). These intensive exploitations of a few tree species, carried out without knowledge of their growth rates, population structures, and regeneration processes, have locally exhausted merchantable stocks and caused the disappearance of some timber species from local and regional markets within only a few decades (Ayres 1993; Higuchi et al. 1994; Worbes et al. 2001; Lima et al. 2005). Many of these unsustainable timber extractions include also trees with diameters below the 45 cm DCL (Albernaz and Ayres 1999; Anderson et al. 1999b), which accelerates the degradation of species population structure. Macedo and Anderson (1993) report wood extraction of 145 m^3 ha^{-1} of *Virola surinamensis* in inundation forests of the Preto River at the Marajó Island representing 90% of the original *Virola*-population and 56% of the entire floodplain forest growing stock.

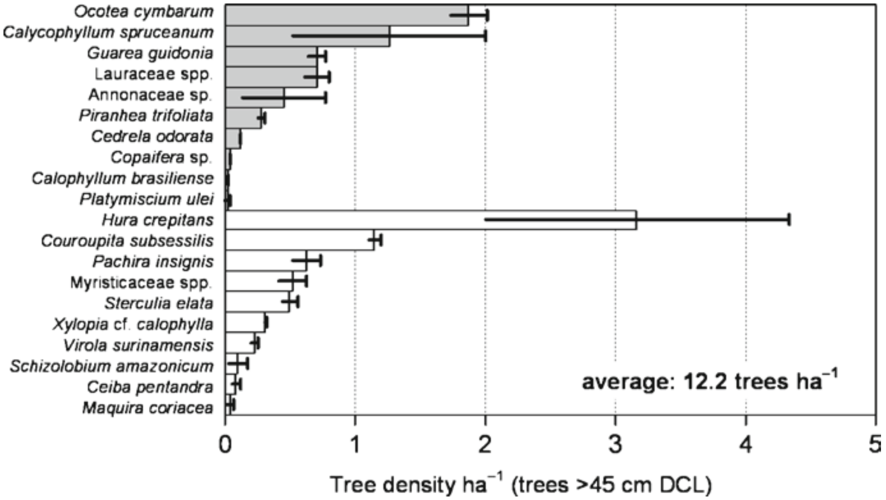

Fig. 20.1 Tree density of high-density (*grey bars*) and low-density (*white bars*) tree species above the diameter cutting limit (DCL) of 45 cm in várzea forests of the Mamirauá Sustainable Development Reserve (MSDR) (mean and standard deviation of two inventories with a total area of 342.9 ha) (Data: 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 20.2 Timber exploitation in the western Amazon basin (Brazil, Peru) (Schöngart 2003)

Source	Gethal S.A. (unpublished)		Albernaz and Ayres (1999)		Kvist and Nebel (2001)			
Location	Madeira, Juruá, Purus Rivers		MSDR Japurá/Solimões Rivers		Loreto (Peru)		Ucayali (Peru)	
Year	1990s		1993/1994		1996		1996	
Category	Roundwood[a]		Roundwood[b]		Roundwood		Lumber	
Unit	Volume		Logs		Volume		Volume	
	m^3 year^{-1}	(%)	m^3 year^{-1}	(%)	m^3 year^{-1}	(%)	m^3 year^{-1}	(%)
High-density tree species								
Manilkara sp.	9,294	12.9						
Cedrela odorata	187	0.3	86	1.7	27,154	15.7	25,670	20.8
Ocotea cymbarum			589	11.4				
Copaifera spp.	3,489	4.8	61	1.2	8,295[c]	4.8	19,686[c]	15.9
Sum	20,256	28.1	1,259	24.4	28,482	23.3	47,966	38.8
Low-density tree species								
Hura crepitans	13,368	18.5	1,765	34.1	3,191	1.9	26,719	21.6
Maquira coriacea	8,425	11.7	274	5.3	5,031	2.9		
Ceiba pentandra	5,853	8.1	469	9.1	60,323	34.8	3,426	2.8
Virola spp.	2,062	2.9	872	16.8	27,884	16.1	17,247	14.0
Sum	28,708	41.0	3,380	65.3	96,429	55.7	47,392	38.4
Other timber species	22,310	30.9	539	10.3	36,392	21.0	28,089	22.8
Total	72,274	100	5,178	100	173,183	100	123,447	100

[a] Sum of four concessions (Manicoré, Humaitá, Itamaratí und Lábrea)

[b] Average of the exploitations in the years 1993 and 1994

[c] *Copaifera paupera* (Herzog) Dwyer

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, IDSM)

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

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

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

20.2.3 Marketing and Wood Prices

The traditional marketing of timber in the floodplain forests is practiced in various ways (Albernaz and Ayres 1999). Traders (*padrão*) often operate as middle man in the area where they customarily trade, often barter, with local riparian communities for natural products, buying at low prices against selling at high prices. This form of trading is common for local populations living far away from regional 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 2010). 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, 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 m^{-3} for *H. crepitans*, US$ 20.00 m^{-3} for *M. coriacea*, and US$ 35.00 m^{-3} 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 exploitations 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, many of them in várzea floodplains along the Solimões, Amazonas, Juruá, and Madeira Rivers (IEB 2007).

Similar concepts of participatory communal forest management in várzea floodplains are also pursued in the MSDR at the confluence of the Solimões and the Japurá Rivers, approximately 70 km northwest of the city of Tefé, in the Central Amazon (Queiroz and Peralta 2010). The MSDR comprises 11,240 km² of várzea floodplains. The reserve was the first conservation unit in the Brazilian várzea, established in 1990 as an Amazonas State Ecological Station and transformed into a Sustainable Development Reserve in 1996 by the State's Governor as a new category of conservation unit in Brazil (Queiroz and Peralta 2010). Together with the Amanã Sustainable Development Reserve, Jaú and Anavilhanas National Parks, the MSDR forms the "Central Amazon Conservation Complex" with a total area of about 6 million hectares. This region was declared as a world natural heritage site by UNSECO in the year 2000 and recognition was extended in 2003 (Ayres et al. 2005). Since 1992, numerous community-based management projects have been initiated in the focal area of the MSDR (2,600 km²) based on socio-economic and biological-ecological studies of fishery, agriculture, agro-forestry, eco-tourism, and forestry (Sociedade Civíl Mamirauá 1996; Ayres et al. 1998; Queiroz and Peralta 2010).

The community forest management program *Manejo Florestal Comunitário* (PMFC) was established in 1998 and operated the first time in 2000. Since then, more than 30 cooperatives (*associação comunitária*) set up to perform controlled timber extractions have been founded within the focal area of the MSDR. Timber harvesting permission requires a management plan (Forest Code No. 4,711 from 15 September 1965) authorized by environmental agencies (Schöngart 2003) and based on a forest inventory, which considers in the MSDR all trees of timber species >25 cm diameter in the areas selected for harvest. The mean annual management area allocated for sustainable timber and wood harvesting is about 25 ha per cooperative. Within this area, a polycyclic harvesting system (Lamprecht 1989; Dawkins and Philip 1998; Whitmore 1993) in the sense of a Selection Silvicultural Management System (Wyatt-Smith 1995; Bruenig 1998), adapted from the CELOS system in Surinam (de Graaf et al. 2003), is permitted. The aim is to keep an all-ages stand through selective tree cuttings at shorter intervals (felling cycle) and by establishing a DCL. The felling cycle defines the interval in years between successive timber harvests in the same coupe area. Due to the harvest of only a few selected trees above the established DCL, the uneven-age structure of the forest is maintained by the establishment of seedlings on the ground in small gaps and saplings in the understorey. To achieve a more or less constant annual harvest, the total area for forest management is divided into several blocks of similar size and growing stock quality corresponding to the number of years of the felling cycle (annual managament area). Thus far, forest management in the MSDR applies a DCL of 50 cm, a felling cycle of 25 years, and a maximum yield of 25 m^3 ha^{-1} restricted to 3 trees ha^{-1} including floats. Furthermore, 10% of the emerging A-storey trees (Richards 1996) of commercial species, as a rule above the DCL, must remain in the forest to improve the chances for regeneration of timber species (Pires 2004).

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

Queiroz and Peralta 2010). Timber species potentially or actually threatened by extinction, such as *C. brasiliense, C. odorata, C. pentandra, P. ulei, V. surinamensis*, and *Xylopia frutescens*, are excluded from the list of commercial species and totally protected (Worbes et al. 2001). The recently established IN no°5, from 11 December 2006 (IBAMA), enables modified management options. Felling cycles are 25–35 years and periodic yields limited to 30 m^3 ha^{-1} (full yield modality) or alternatively 10 m^3 ha^{-1} every 10 years (low yield modality). In várzea forests yields can exceed 10 m^3 ha^{-1}, but must be restricted to three harvested trees ha^{-1}. The establishment of species-specific DCLs that take into account ecological and technical criteria has also been mandated. If this information is not available for a commercial timber species, a common DCL of 50 cm is applied.

Economic activities in the várzea, such as agriculture, fishery, and timber extraction, and consequently the income, are associated with water-level fluctuations. Commercial fishing is possible during low-water levels, when fish stocks are concentrated in the remaining water bodies (Fig. 20.4). Agriculture is practiced during the terrestrial phase on higher elevations, where flooding is shortened and crops have enough time to mature and ripen (Junk et al. 2010a). Forestry activities are mainly restricted to the aquatic phase, when the forests can easily be accessed and transport costs are low (Barros and Uhl 1995; Albernaz and Ayres 1999). In the MSDR, 70% of the annual income is derived from fishery, about 20% from agriculture (mainly cassava), and only 5% from timber extraction (Sociedade Civil Mamirauá 1996). For domestic households, this leads to high incomes during the terrestrial phase and low incomes during the flooded period (Fig. 20.4).

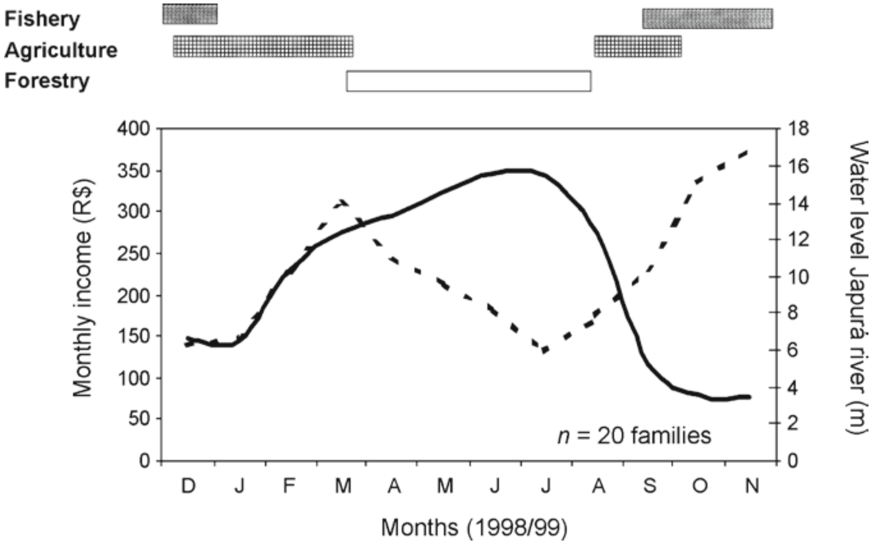

Fig. 20.4 Performance of economic activities in the várzea and average monthly income (*dotted line*) of 20 households in the MSDR in relation to water-level fluctuations of the Japurá River (*black line*) (Data: Sociedade Civíl Mamirauá 1996; Albernaz and Ayres 1999; Mamirauá Institute for Sustainable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

Inspite of the small financial share in household income, the controlled community-based forest management is making a welcome contribution to the meagre budgets of households in the Amazonian várzea, especially when the monthly income is seasonally very low (Queiroz and Peralta 2010). As timber harvesting and selling is authorized by environmental agencies the wood and timber prices (per meter cube) are several times higher than those obtained in unauthorized, illegal operations (Table 20.3). Roundwood prices are given in Brazilian Reais (R$)

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

(R$ m^{-3})	Middle Solimões (MSDR)	Middle Solimões (MSDR)	Upper Solimões
Period/year	1994	2004	
Low-density tree species	Illegal exploitation	Legal management	
Assacú (*Hura crepitans*)	1.45–5.00[a] 0.75–2.50[b]	28.00	40.00
Muiratinga (*Maquira coriacea*)	3.30–10.30[a] 1.75–5.15[b]	36.00	80.00
Sumaúma (*Ceiba pentandra*)	3.30–10.30[a] 1.75–5.15[b]		50.00
Macacarecuia (*Couroupita subsessilis*)	1.20–3.00[a] 2.40–6.00[b]	28.00	
Abiorana (*Pouteria* sp.), Araparí (*Macrolobium acaciifolium*), Faveira (*Vatairea guianensis*), Tacacazeiro (*Sterculia elata*), Ucuúba (*Virola* spp.), Paricarana (*Schizolobium amazonicum*)		36.00	
Caxinguba (*Ficus insipida*)		32.00	
High-density tree species			
Cedro (*Cedrela odorata*)			120.00
Jacareúba (*Calophyllum brasiliense*)	4.23[b]–8.45[a]		80.00
Coração de negro (*Swartzia* sp.), Gitó (*Guarea guidonia*), Louro abacate (*Aniba guianensis*), Louro amarelo (*Aniba riparia*), Louro inamuí (*Ocotea cymbarum*), Louro preto (*Licaria* sp.), Mulateiro (*Calycophyllum spruceanum*), Piranheira (*Piranhea trifoliata*), Tanimbuca (*Terminalia dichotoma*)	4.23[b]–8.45[a]	48.00	

[a] Diameter <50 cm

[b] Diameter >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 m^{-3} (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) m^{-3}. 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) m^{-3} for low-density timber and R$ 170.00 (US$ 80.95) m^{-3} for high-density timber, (US$ 1.00 = R$ 2.10) (data: Mamirauá Institute for Sustainable Development, IDSM/PMFC).

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 (year 2007) (Tables 20.4–20.6). The income varied considerably between the three projects, from R$ 27.75 (US$ 13.21) to R$ 102.72 (US$ 48.91) ha^{-1} yr^{-1}. 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 mean annual management area of 25 ha is then between R$ 693.82 (US$ 330.39) and R$ 2,567.89 (US$ 1,222.81). 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).

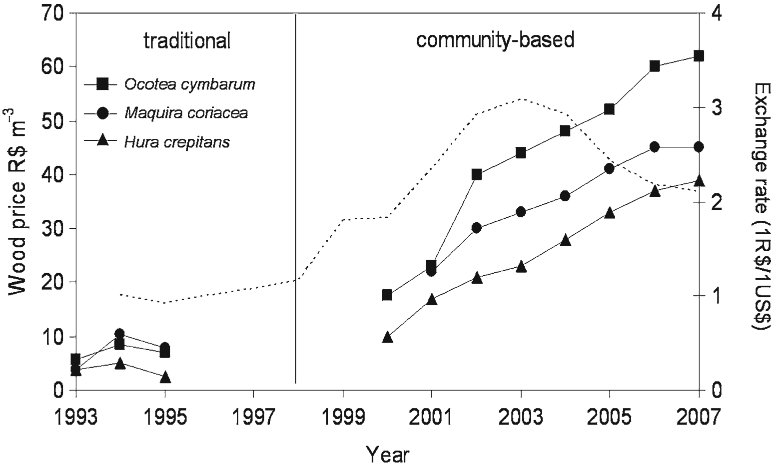

Fig. 20.5 Development of roundwood prices (R$ m^{-3}) in the MSDR from 1993 to 2007 for the high-density tree species *Ocotea cymbarum* and low-density tree species *Maquira coriacea* and *Hura crepitans* (Data: Albernaz and Ayres 1996; Mamirauá Institute for Sustainable Development, IDSM/PMFC). The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

Table 20.4 Timber extraction from community-based forest management of the 19.5-ha high várzea forest "Traíra Lake", MSDR (Sector Tijuaca, community Nova Betel) (Data: Brampton 2001, Mamirauá Institute for Sustainable Development, IDSM/PMFC)

Local name	Scientific name	Trees ha^{-1}	Volume (m^3 ha^{-1})	Wood price 2007 (R$ m^{-3})	Value (R$)
Low-density tree species					
Assacú	*Hura crepitans*	0.67	5.21	39.00	203.12
Macacarecuia	*Couroupita subsessilis*	0.21	0.65	35.00	22.78
Subtotal		0.88	5.86		225.90
High-density tree species					
Louro inamuí	*Ocotea cymbarum*	2.36	3.80	62.00	235.50
Mulateiro	*Calycophyllum spruceanum*	0.72	3.26	62.00	202.47
Gitó	*Guarea guidonia*	0.26	0.30	62.00	18.47
Piranheira	*Piranhea trifoliata*	0.15	0.19	62.00	11.48
Subtotal		3.49	7.55		467.92
Floats					
Munguba	*Pseudobombax munguba*	0.10	0.24		
Bolacheira	*Apeiba* sp.	0.10	0.11		
Subtotal		0.20	0.34		
Total		*4.57*	*13.75*		*693.82*
	m^3 ha^{-1} yr^{-1}		0.55	R$ ha^{-1} yr^{-1}	27.75

Table 20.5 Timber extraction of the community-based forest management in the MSDR of the 9.0 ha high várzea forest "Redondo Lake" (Sector Tijuaca, community Nova Betel) (Data: Brampton 2001, Mamirauá Institute for Sustainable Development, IDSM/PMFC)

Local name	Scientific name	Trees ha^{-1}	Volume (m^3 ha^{-1})	Wood price 2007 (R$ m^{-3})	Value (R$)
Low-density tree species					
Assacú	*Hura crepitans*	2.89	47.04	39.00	1,834.56
Tacacazeiro	*Sterculia elata*	0.22	2.05	45.00	92.25
Subtotal		3.11	49.09		1,926.81
High-density tree species					
Louro inamuí	*Ocotea cymbarum*	1.00	1.79	62.00	182.90
Mulateiro	*Calycophyllum sprucenaum*	0.22	4.77	62.00	295.74
Gitó	*Guarea guidonia*	0.22	2.95	62.00	110.98
Piranheira	*Piranhea trifoliata*	0.11	0.83	62.00	51.46
Subtotal		1.55	10.34		641.08
Floats					
Bolacheira	*Apeiba* sp.	0.33	1.38		
Subtotal		0.33	1.38		
Total		*4.99*	*60.81*		*2,567.89*
	m^3 ha^{-1} yr^{-1}		2.43	R$ ha^{-1} yr^{-1}	102.72

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

Local name	Scientific name	Trees ha^{-1}	Volume (m^3 ha^{-1})	Wood price 2007 (R$ m^{-3})	Value (R$)
Low-density tree species					
Assacú	*Hura crepitans*	1.31	10.29	39.00	401.26
Ararí	*Macrolobium acaciifolium*	0.28	0.96	43.00	41.16
Macacarecuia	*Couroupita subsessilis*	0.10	0.97	35.00	33.83
Muiratinga	*Maquira coriacea*	0.10	0.40	45.00	17.78
Mungubarana	*Pachira insignis*	0.14	0.61	33.00	20.20
Paricarana	*Schizolobium amazonicum*	0.18	1.12	45.00	50.22
Seringa barriguda	*Hevea spruceana*	0.04	0.05	30.00	1.53
Tacacazeiro	*Sterculia elata*	0.18	1.71	45.00	77.01
Subtotal		2.33	16.11		642.99
High-density tree species					
Abiorana	*Pouteria* sp.	0.28	2.50	43.00	107.58
Perereca	*Dulacia candida*	0.04	0.14	62.00	8.60
Louro inamuí	*Ocotea cymbarum*	0.95	3.12	62.00	193.90
Louro preto	*Licaria* sp.	0.07	0.20	62.00	12.58
Louro abacate	*Aniba guianensis*	0.04	0.34	62.00	20.72
Louro amarelo	*Aniba riparia*	0.10	0.22	62.00	13.70
Gitó	*Guarea guidonia*	0.64	2.72	62.00	168.66
Mulateiro	*Calycophyllum sprucenaum*	0.07	0.35	62.00	21.80
Piranheira	*Piranhea trifoliata*	0.07	0.48	62.00	29.89
Tanimbuca	*Terminalia dichotoma*	0.18	0.80	62.00	49.61
Castanharana	*Eschweilera ovalifoila*	0.07	0.34	43.00	14.58
Faveira	*Vatairea guianensis*	0.10	0.34	43.00	14.56
Coração de negro	*Swartzia* sp.	0.07	0.16	62.00	10.01
Subtotal		2.67	11.71		666.19
Total		*5.00*	*27.82*		*1,309.18*
m^3 ha^{-1} yr^{-1}			1.11	R$ ha^{-1} yr^{-1}	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 m^3 (Albernaz and Ayres 1999). This corresponds to 23 trees in average per person with an average volume of 2.9 m^3 per tree and 67.5 m^3 per person. In 2003 about 98 persons were involved in the PMFC with a total yield of 949 trees comprising a volume of 8,507 m^3. 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 m^3) per person as under uncontrolled conditions. The improvement of the management system and the increasing timber prices (Fig. 20.5)

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

	Traditional timber harvesting	Community forest management
Year	1993	2003
Extracted trees	6,897 trees	949 trees
Extracted volume	20,235 m³	8,507 m³
Average volume per tree	2.93 m³	8.96 m³
People involved	300	98
Trees per person	23.0 trees	9.7 trees
Volume per person	67.5 m³	86.8 m³
Income per person	219.63	1,049.94

resulted in an almost fivefold higher income per person under controlled management conditions when compared to the traditional harvesting system. Additionally, training of the local communities by the technical staff of the PMFC in performing forest inventories, logging, skidding, and marketing increases the efficiency of community forest management, limits damages to the remaining trees, and reduces the risks to human health (Pires 2004) and possibly will increase net returns. This kind of development renders community forest management a socially and economically important component of communal life, which contributes significantly to improve the financial situation, social coherence and welfare of riparian communities, especially noticeably during the aquatic phase, when fishing and agriculture are limited (Fig. 20.4).

20.4 Discussion and Conclusions

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

Generally, the conditions for sustainable and integrated forest management and conservation are more favourable in the várzea than in the terra firme, as the former consists of highly productive forest ecosystems (Schöngart et al. 2010), has plenty of commercial timber species and timber harvesting is simple and costs are low (e.g., Barros and Uhl 1995, 1999). Rapid depletion of nutrient stocks in the soils after removal of large 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 long-term fertility and utility of floodplain soils (Furch 1997, 2000). The total timber harvest is between 4.57 and 5 trees ha^{-1} which yields 13.8–60.9 m^3 ha^{-1} per felling cycle or 0.55–2.37 m^3 ha^{-1} yr^{-1} (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 among the most productive and manageable tropical forest ecosystems (Nebel et al. 2001a; Schöngart et al. 2010). Volume increments of mature várzea forests are in the range of 10.1–16.2 m^3 ha^{-1} yr^{-1}, and young successional stages have even higher annual volume increments of 43.7–51.9 m^3 ha^{-1} yr^{-1} (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 ha^{-1} yr^{-1}) more or less corresponds to the annual wood biomass production of timber (0.50 Mg ha^{-1} yr^{-1}). 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 rare (Nebel et al. 2001b; Schwartz et al. 2002; Sokpon and Biaou 2002; Nebel and Meilby 2005; Brienen and Zuidema 2006a,b, 2007; Schöngart et al. 2007; Schöngart 2008). Forest management in the várzea forests, as in the tropics and elsewhere generally, needs a scientific database describing species-specific and site-specific growth rates, tree ages, and regeneration processes to achieve sustainable timber resource management.

For the várzea, the restrictions established in IN n°5 of IBAMA do not reflect scientific data. By contrast, it is already a progress to use the best available data to set tentatively felling cycles ranging from 10 to 35 years. The IN n°5 further demands species-specific DCLs based on supporting studies of population structure (diameter distribution), ecological aspects (reproduction, highest productivity) and technical market demands (prices for different diameter classes, minimum diameters for the various forms of timber processing, timber qualities for different uses, and so on). Only by step-wise implemented rules and adaptive management can we rationally approach and approximate sustainable management and conservation. Nonetheless, we must be aware that hasty application of management criteria for certain timber species remains a high-risk gamble as long as data on forest processes, such as tree growth and natural regeneration, are inadequate. The genetic to architectural forest population structure is likely to suffer, genetic resources decline and species are lost, and the forest ecosystem becomes more vulnerable particularly to the impacts of climate change. Therefore, immediate efforts are crucial to obtain realistic estimations of tree age, increment rates, volume production, population structure and regeneration processes of tree species growing under varying edaphic, hydrologic, and climatic conditions, as shown by the concept on growth-oriented logging (GOL) (Schöngart 2010). This and similar approaches that increase the welfare of the involved local populations and maintain the ecosystem's multiple services are the only way that the long-term ecological and socio-economic viability of the management of timber resources can be safeguarded.

Acknowledgment We thank Eberhard F. Bruenig and Plinio Sist for their careful review and valuable comments on this chapter.

Chapter 21
Growth-Oriented Logging (GOL): The Use of Species-Specific Growth Information for Forest Management in Central Amazonian Floodplains

Jochen Schöngart

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Abstract So far, timber resources in central Amazonian floodplain forests are managed by selective logging with a felling cycle of 25 years and a diameter cutting limit (DCL) of 50 cm. However, these time and diameter limitations are estimations or legal restrictions rather than being derived from scientific data. From 14 tree species of nutrient-rich white-water (várzea) and nutrient-poor black-water (igapó) floodplain forest in central Amazonia wood growth in diameter and volume was modelled using tree-ring analyses. Cumulative diameter growth curves indicated periods between 15 and 261 years for species to pass over the DCL of 50 cm. From volume growth models the minimum logging diameter (MLD) was defined as diameter at the age of maximum current volume increment rates. For the majority of the analysed tree species the MLD was higher than the DCL of 50 cm. Felling cycles, estimated as the mean passage time through 10 cm diameter classes until reaching the MLD, indicated large variations from 3 to 53 years between tree

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species. Tree species which occur in both floodplain system present significantly lower diameter increment rates in the igapó than in the várzea due to the contrasting nutrient status. The sustainable use of timber resources in the igapó is, under current management options, not practicable and this ecosystem should be therefore excluded from timber resource management and permanently protected. The várzea is a dynamic system with highly productive forest ecosystems which favours the development of an integrated sustainable forest management. However, such a timber resource management must be species-specific. Based on tree ages, increment rates, volume production and population structure of commercial tree species the GOL concept (Growth-Oriented Logging) was developed to achieve a higher level of sustainability for the timber resource management in várzea forests.

21.1 Introduction

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).

For centuries the várzea floodplains have been settled and used, largely because of its easy accessibility, high soil fertility, and richness in natural resources (Junk 2000a). Most commercial tree species occur in high-várzea forests (Worbes et al. 2001) which become flooded to a height of annually less than 3 m above forest floor. These forests cover only 8–10% of the central Amazonian várzea (Wittmann et al. 2002b) and are threatened by strong pressures to increase timber logging and to converse large areas to pastures, agricultural lands, and settlements. Another forest type, the low várzea, occur on about 40% of the floodplains in central Amazonia, comprises fewer commercial tree species and is inundated annually by a water column of 3–6 m above the ground (Wittmann et al. 2002b). Due to its longer inundation period, the low várzea suffers less conversion pressure, because the agriculturally permissive period is too short. Forest management can be more readily performed on this forest type, since flooding occurs regularly each year, thus guaranteeing access to harvested trees for skidding and transport (Schöngart and Queiroz 2010). An increasing number of tree species of the low várzea forests is becoming commercialized; for example, in the Peruvian várzea, tree species of the low várzea, such as *Macrolobium acaciifolium*, *Paramachaerium ormosioides*, and *Ficus insipida*, already are exploited by the timber industry (Schöngart 2003). Martini et al. (1998) pointed out the low-várzea tree species *Vatairea guianensis*, *Pseudobombax munguba*, and *Pouteria elegans* as commercially important. High-density species from the low várzea, including *Tabebuia barbata*, *Chrysophyllum argenteum*, *Eschweilera albiflora*, and *Piranhea trifoliata*, as well as the wood of some low-density species, such as *P. munguba* and *Luehea cymulosa*, are harvested by local inhabitants (Brampton 2001; Kvist et al. 2001; Wittmann et al. 2009; Wittmann and Oliveira Wittmann 2010) for substantial use.

The várzea is a dynamic landscape patchwork of water bodies, aquatic and terrestrial macrophytes and forests as a result of erosion and sedimentation processes (Salo et al. 1986; Irion et al. 1997; Kalliola et al. 1991; Worbes et al. 1992; Schöngart et al. 2003; Wittmann et al. 2004; Wittmann et al., 2010). Primary succession initiates at sites with high sedimentation rates, i.e., next to a river. Due to geomorphological and environmental modifications, young pioneer stands (up to 20 years of age) are able to develop into early secondary stages (20–40 years old). These are followed by late secondary (50–80 years old) and late successional stages at higher elevated sites with relatively longstanding stable environmental conditions, resulting in stand ages up to 400 years old (Wittmann et al. 2004; Wittmann et al. 2010). Along this successional gradient, the wood densities of tree species increase whereas diameter increment rates decrease, reflecting the substitution of pioneer species by those that are long-living and by climax species (Swaine and Whitmore 1988; Worbes et al. 1992; Schöngart 2003; Schöngart et al. 2010). With increasing stand age, tree density declines and tree species richness increases, leading to changes in the canopy architecture, i.e., increasing stand height and crown size and decreasing crown number (Terborgh and Petren 1991; Wittmann et al. 2002b; Schöngart et al. 2003) leading to changing optical and aerodynamic properties of the canopy (Wittmann et al. 2010).

Most studies dealing with sustainable forest management in the várzea have based their approach to sustainability on data describing species composition and structure and on evaluation of the value of timber and NWFPs, for instance, in the Amazon Estuary (Bentes-Gama et al. 2002; Gama et al. 2005a,b; Fortini et al. 2006). However, scientific reliable knowledge from 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. 2001d), regeneration (Nebel et al. 2001c), estimations of net primary production (Nebel et al. 2001a), 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 n°5 (11 December 2006) defines diameter cutting limits (DCLs) and felling cycles (Schöngart and Queiroz 2010) for regular management plans with a felling cycle of 25–35 years and maximum yields of up to 30 $m^3\ ha^{-1}$ or, alternatively, management plans with low yield intensities (< 10 $m^3\ ha^{-1}$) applying a shorter felling cycle of 10 years (in várzea yields can exceed 10 $m^3\ ha^{-1}$, but must be restricted to 3 harvested trees ha^{-1}). The IN n°5 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). However, the technical and logistic improvements of RIL are not sufficient to guarantee sustainable management of timber resources (Schöngart and Queiroz 2010).

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 Fichtler 2010). The derived management criteria are compared with currently practised timber resource management in the central Amazonian várzea (Schöngart and Queiroz 2010) and, together with data from population structure of the studied tree species, new management concepts are developed. In this chapter, the GOL concept is also extended to the nutrient-poor floodplains (igapó) to see how the contrasting nutrient status (Furch 1997, 2000) affects diameter growth and the derived management criteria of its commercial tree species.

21.2 Material and Methods

21.2.1 Tree-Ring Analysis and Growth Modeling

The várzea sites are situated in the Mamirauá Sustainable Development Reserve (MSDR) described more in detail by Queiroz and Peralta (2010). The study sites of the igapó are located in the Amanã Sustainable Development Reserve (ASDR) and

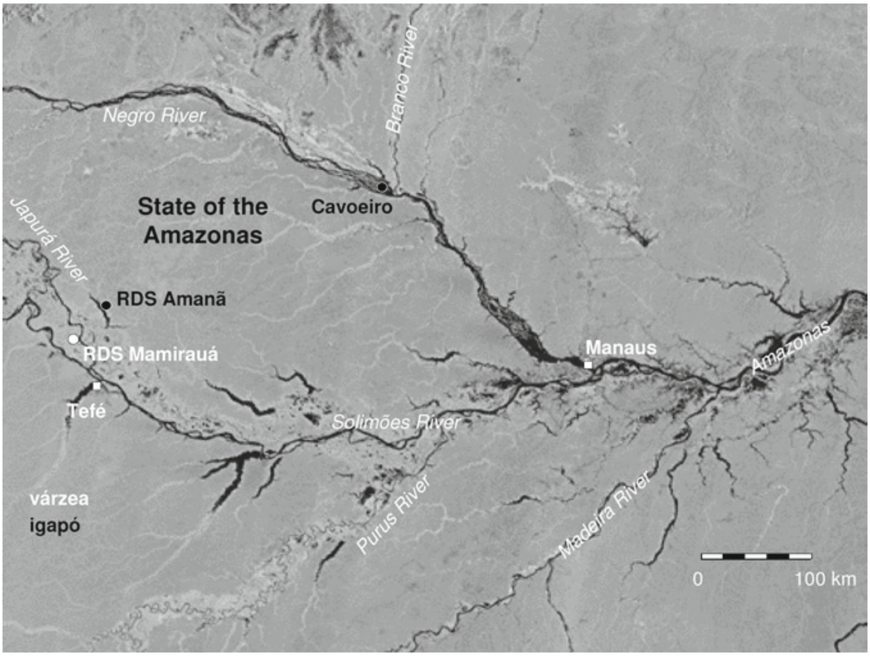


Fig. 21.1 Map of the central Amazon region indicating study sites in the nutrient-poor black-water floodplains (igapó, black circles) and the nutrient-rich white-water floodplains (várzea, white circle)

upon the confluence of the Negro and Branco Rivers (Fig. 21.1). From 14 tree species, 137 stem disks and 170 cores were collected from emergent individuals for tree-ring analyses. In the MSDR wood samples were obtained from 12 tree species comprising *Ficus insipida* (Moraceae) in a 20-year-old early secondary stage (Schöngart et al. 2007) and from *Pseudobombax munguba*, *Luehea cymulosa* (both Malvaceae), *Ilex inundata* (Aquifoliaceae), *Macrolobium acaciifolium*, and *Albizia subdimidiata* (both Fabaceae) in a 50-year-old late secondary stage. In the over 100-year-old late successional stages *Tabebuia barbata* (Bignoniaceae), *Eschweilera albiflora* (Lecythidaceae), *Piranhea trifoliata* (Euphorbiaceae), *Pouteria elegans*, *Chrysophyllum argenteum* (both Sapotaceae), and *Sloanea terniflora* (Elaeocarpaceae) were sampled (Schöngart 2003). The study sites are located in the low várzea almost at the same elevation and are annually flooded between 120–150 days, by an average depth of 336–465 cm (Schöngart 2003). In the igapó wood samples were obtained in pristine floodplain forests from *M. acaciifolium* (ASDR) (Schöngart et al. 2005) and *Calophyllum brasiliense* (Clusiaceae) (*Cavoeiro*). At both igapó sites the average water column passes over 6 m. The commercial tree species were classified using a threshold of about 0.60 g cm^{-3}, into low-density (*madeira branca*) and high-density (*madeira pesada*) tree species (Schöngart 2003; Schöngart and Queiroz 2010).

The wood samples were analyzed in the Dendroecological Laboratory of the National Institute for Amazon Research (INPA) in Manaus. The cores were clued on wooden supports and polished together with the stem disks with sand paper of decreasing grain size from 40 to 600 grits and cleaned afterwards with compressed air. Tree rings were dated by their wood anatomical structure using a binocular. More details on wood anatomy and tree ring analysis were previously described (Schöngart et al. 2004, 2005, 2007; Worbes and Fichtler 2010). Ring width was measured with a digital measuring device (LINTAB) to the nearest 0.01 mm supported with software for tree-ring measurement, analysis and presentation (TSAP-Win, Rinntech, Heidelberg, Germany).

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

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

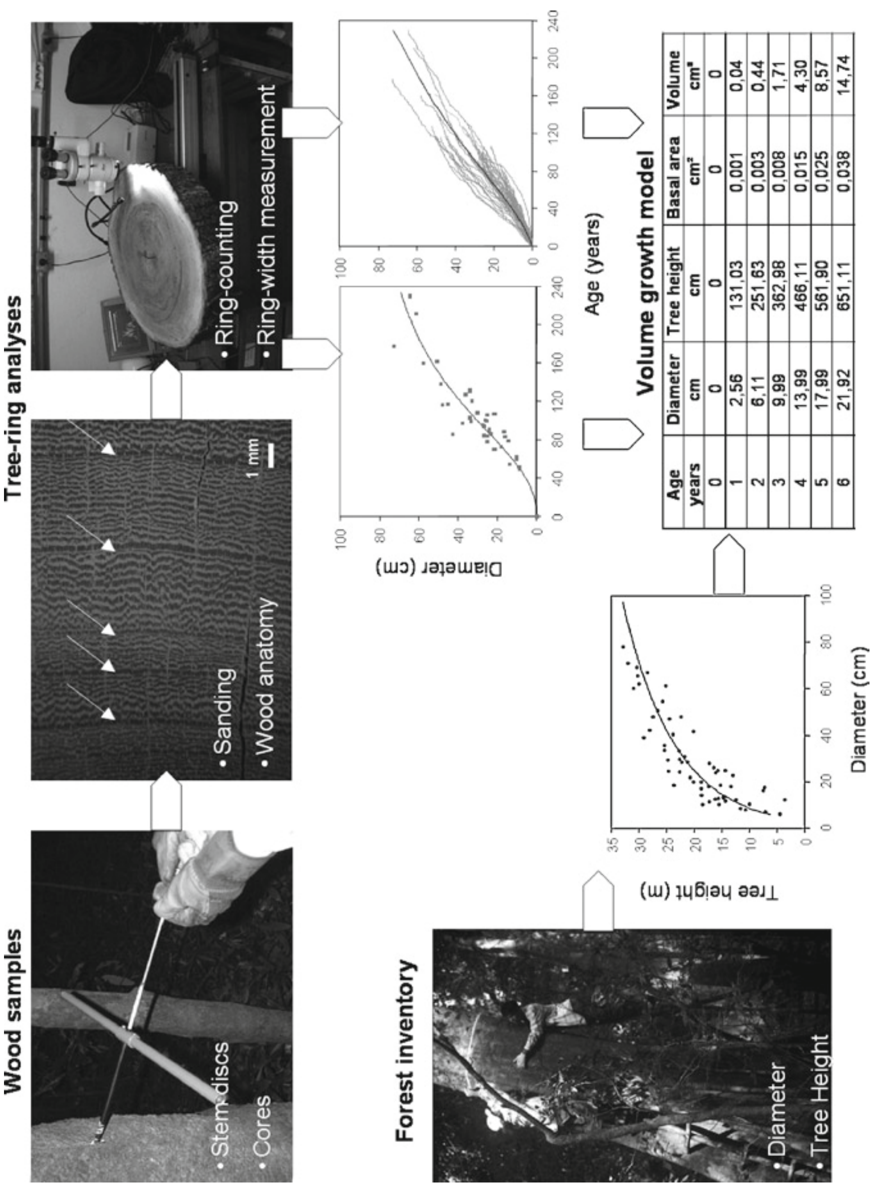
Height growth of a tree species was estimated by combining the age-diameter relationship and the relationship between diameter and tree height *h* measured in the field fitted to a non-linear regression model (Nebel 2001; Nebel et al. 2001b; Schöngart et al. 2007):

$$h = d \times \mathrm{a} \,/\, \left(d + \mathrm{b}\right) \tag{21.2}$$

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

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

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



Age years	Diameter cm	Tree height cm	Basal area cm^2	Volume cm^3
0	0	0	0	0
1	2,56	131,03	0,001	0,04
2	6,11	251,63	0,003	0,44
3	9,99	362,98	0,008	1,71
4	13,99	466,11	0,015	4,30
5	17,99	561,90	0,025	8,57
6	21,92	651,11	0,038	14,74

Fig. 21.2 Growth modeling 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$_t$ along the life-span of a tree by diameter (*d*), tree height (*h*) and a form factor (*f*) of 0.6 ($V_t = \pi \times (d_t/2)^2 \times h_t \times f$)

21.2.2 Definition of Management Criteria

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

$$CAI_V = CGW_{V(t+1)} - CGW_{V(t)} \tag{21.4}$$

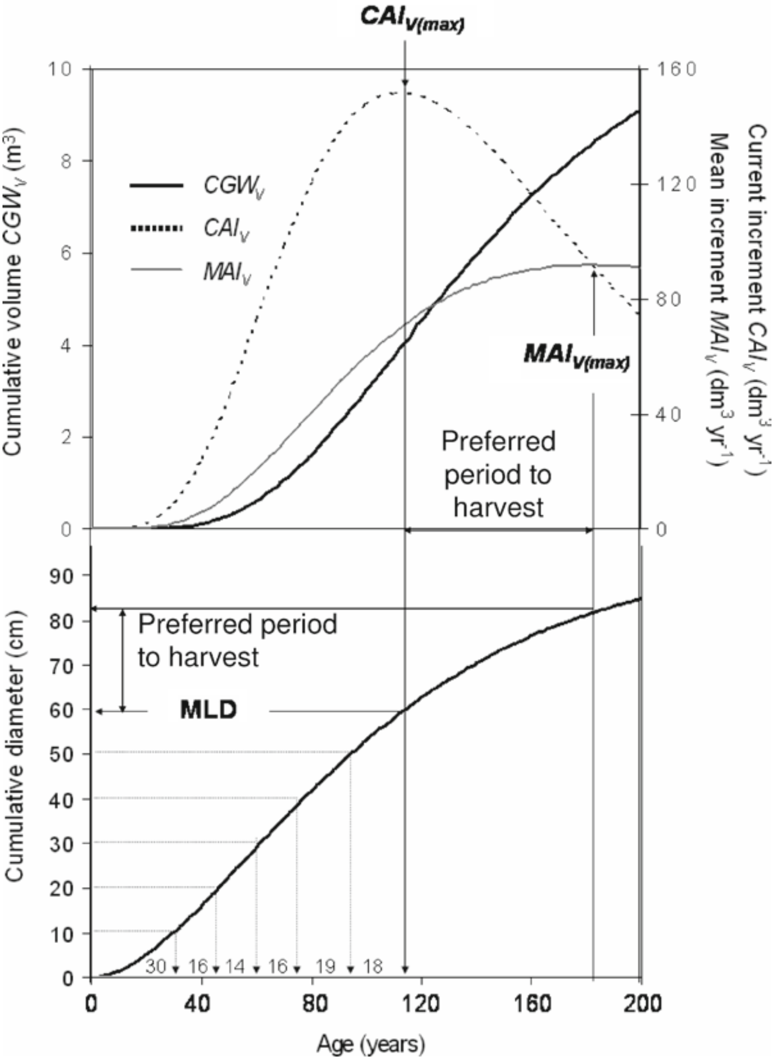


Fig. 21.3 Model of cumulative volume growth (CGW_V) for a tree species and the derived current (CAI_V) and mean (MAI_V) annual volume increment rates. The preferred period for harvest is between the maximum CAI_V and MAI_V. The diameter at the age of the maximum CAI_V is defined as the minimum logging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

$$MAI_V = \frac{CGW_{V(t)}}{t} \quad (21.5)$$

Where CGW_V is the cumulative volume growth in different years t over the entire life span.

From the volume growth model and volume increment rates, criteria for a species-specific management were derived. The model in Fig. 21.3 indicate and increasing CAI_V with increasing diameter and age. To achieve an optimal volume production a tree should be harvested between the optimum of the CAI_V ($CAI_{V(max)}$) and the optimum of the MAI_V ($MAI_{V(max)}$). This time difference was defined as preferred period for harvest (Schöngart 2008). Harvests before the $CAI_{V(max)}$ and after $MAI_{V(max)}$ would lead to an inefficient use of the growth potential of a tree species. The minimum logging diameter was defined as diameter at the age in the optimum of the CAI_V ($CAI_{V(max)}$) and can be derived by the specific age–diameter relationship (Schöngart et al. 2007). To estimate the felling cycle the mean time through 10-cm diameter classes until achieving the specific MLD was calculated (Schöngart 2008). This period represented the average time, which an individual needs to grow from one to the next diameter class of 10-cm intervals (Fig. 21.3):

$$Felling\,cycle = age_{(MLD)} / MLD \times 10 \quad (21.6)$$

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

21.3 Results

21.3.1 The Growth Model

All growth models were based on significant relationships between age and diameter as well as diameter and height (Schöngart et al. 2007; Schöngart 2008; Schöngart et al. 2010). 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* 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). The high-density tree species *C. brasiliense* surpasses a DCL of 50 cm only after 261 years in the igapó floodplains.

Because of the higher diameter and height increments the volume growth of low-density tree species is much faster than that of high-density species in the

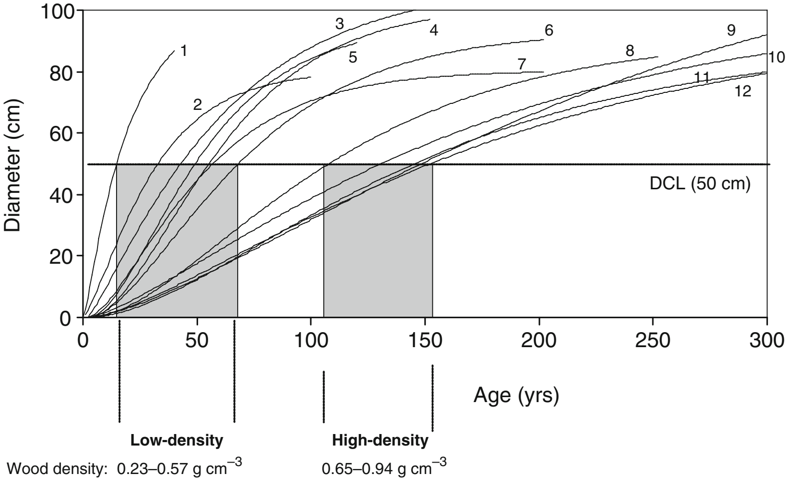


Fig. 21.4 Mean cumulative diameter growth curves of 12 low-density and high-density timber species from the central Amazonian várzea floodplain forests (1 *Ficus insipida*, 2 *Pseudobombax munguba*, 3 *Luehea cymulosa*, 4 *Ilex inundata*, 5 *Macrolobium acaciifolium*, 6 *Albizia subdimidiata*, 7 *Sloanea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

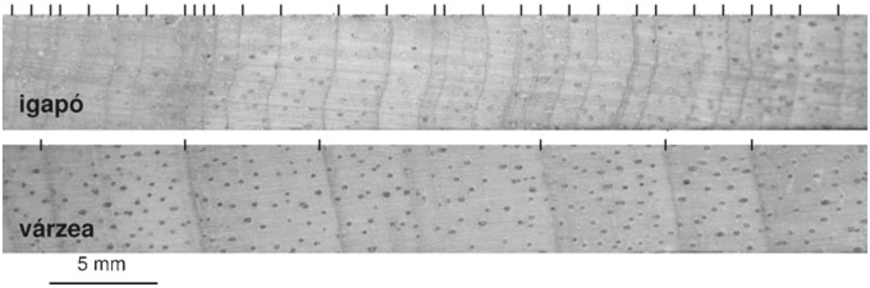


Fig. 21.5 Wood growth of the same species differs significantly in central Amazonian floodplains under contrasting nutrient status as shown by tree-ring series of *Macrolobium acaciifolium* from samples of the igapó (nutrient-poor) and the várzea (nutrient-rich) (Schöngart et al. 2005)

várzea. For example, the first group produces a volume of 6 m³ within 70–100 years, while the high-density timber species need between 200 and 260 years (Fig. 21.7). For selective logging, it is important to know at which age and diameter a tree reaches its growth optimum. The simulation of the diameter (Fig. 21.4) and volume (Fig. 21.7) growth permits the definition of the culmination points of

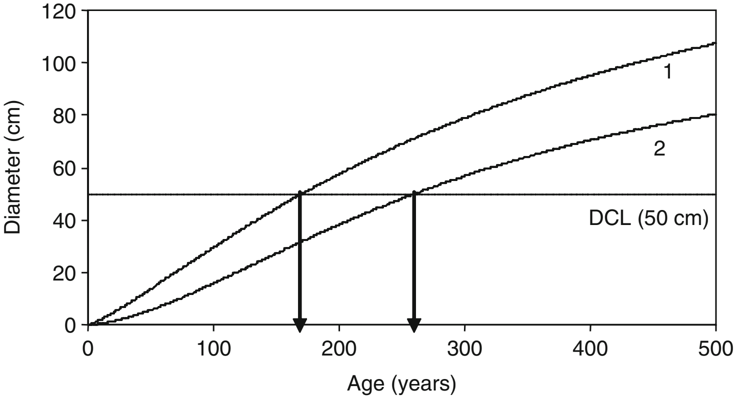


Fig. 21.6 Cumulative diameter growth curves of the low-density timber species *Macrolobium acaciifolium* (1) and the high-density timber species *Calophyllum brasiliense* (2) from the black-water floodplain forests (igapó) of central Amazonia. The diameter cutting limit (DCL) of 50 cm is indicated

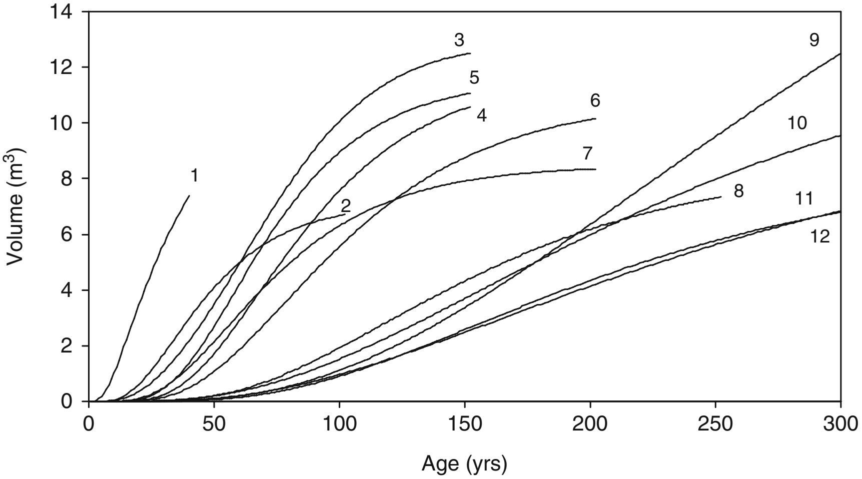


Fig. 21.7 Cumulative mean volume growth curves of 12 low-density and high-density timber species from the central Amazonian várzea floodplain forests (1 *Ficus insipida*, 2 *Pseudobombax munguba*, 3 *Luehea cymulosa*, 4 *Ilex inundata*, 5 *Macrolobium acaciifolium*, 6 *Albizia subdimidiata*, 7 *Sloanea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

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

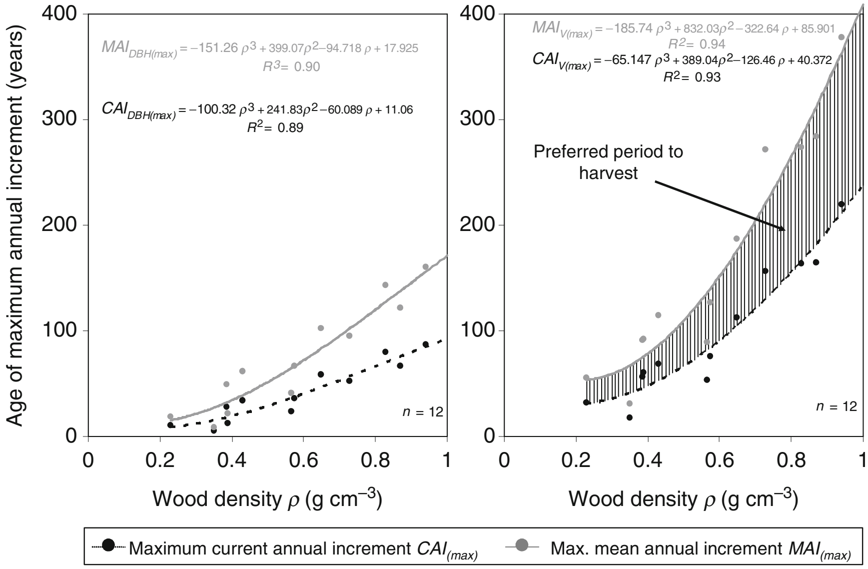


Fig. 21.8 Maximum current and mean annual increment rates in diameter (left) and volume (right) as a function of specific wood density. The hatched area indicates the preferred period for harvest (Schöngart 2003, 2008)

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

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)
VÁRZEA				
Low-density tree species				
Ficus insipida	0.35	55	17.0 ± 3.6	3.3 (2.4–3.7)
Pseudobombax munguba	0.23	47	39.5 ± 2.4	8.2 (7.9–8.9)
Ilex inundata	0.38	59	61.0 ± 9.7	10.5 (8.7–12.0)
Macrolobium acaciifoilum	0.43	62	67.0 ± 5.6	10.5 (9.9–11.7)
Albizia subdimidiata	0.57	49	53.5 ± 7.1	10.5 (9.5–12.4)
Luehea cymulosa	0.39	61	68.5 ± 11.7	11.0 (9.3–13.1)
Sloanea terniflora	0.57	58	82.0 ± 9.1	13.9 (12.6–15.7)
High–density tree species				
Pouteria elegans	0.65	54	120.0 ± 21.8	21.5 (18.2–26.3)
Chrysophyllum argenteum	0.73	58	144.0 ± 22.4	24.1 (21.0–28.7)
Eschweilera albiflora	0.83	53	164.5 ± 44.6	30.9 (22.6–39.5)
Tabebuia barbata	0.87	54	168.5 ± 19.8	30.6 (27.5–34.9)
Piranhea trifoliata	0.94	70	227.0 ± 23.5	32.1 (29.1–35.8)
IGAPÓ				
Low-density timber species				
Macrolobium acaciifolium	0.39	83	326.0 ± 4.5	39.3 (38.6–40.0)
High-density timber species				
Calophyllum brasiliense	0.66	55	293.0 ± 44.0	52.7 (50.8–54.2)

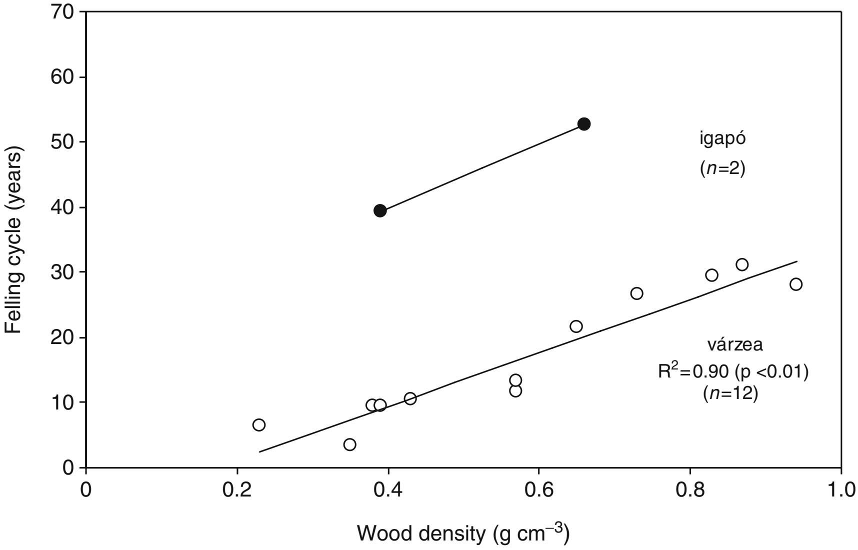


Fig. 21.9 Defined felling cycles of 12 timber species from the nutrient-rich várzea and two species from the nutrient-poor igapó floodplain forest in central Amazonia as a function of the felling cycles established by Brazilian forest legislation (IBAMA, Normative Instruction IN n°5, 11 December 2006)

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 Júnior 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). Stadtler (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 as well as sport fishing (Chao and Prang 1997; Junk et al. 2007; Faria 2005).

Generally, the conditions for sustainable and integrated forest management and conservation are more favourable in the várzea. It is a dynamic system with highly productive forest ecosystems (Schöngart et al. 2010), has plenty of commercial timber

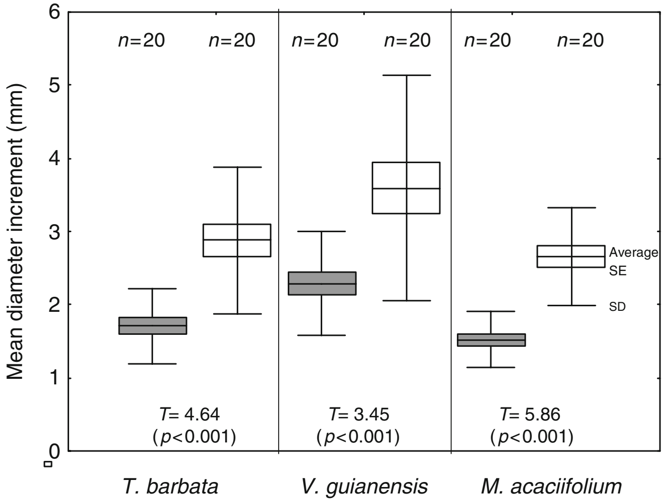


Fig. 21.10 Mean diameter increment of a tree species differs significantly between igapó (grey boxes) and várzea (white boxes) due to the nutrient availability as shown for *Tabebuia barbata*, *Vatairea guianensis* and *Macrolobium acaciifolium* indicated by two sample tests (data: Schöngart et al. 2005;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

species (Wittmann and Oliveira Wittmann 2010) and timber harvesting is characterized by low costs (Schöngart and Queiroz 2010). The annually regular flood-pulse deposits sufficient nutrients to maintain long-term fertility and utility of floodplain soils (Furch 1997, 2000). This favours the development of a integrated sustainable forest management. However, the derived MLDs and felling cycles indicate that the currently practised forest management in the várzea cannot be sustainable, because it apllies only one fixed DCL and felling cycle to harvest a high number of tree species, which vary in lifetime growth rates, tree ages and reproduction strategies. The management in the várzea requires therefore a species-specific management.

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

Forests of the early succession in the várzea (early secondary and late secondary stages) are species poor and have uniform age and architectural structures (Terborgh and Petren 1991; Worbes 1997; Wittmann et al. 2002b; Schöngart 2003; Wittmann et al. 2010). 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 m^3 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 3 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 harvested timber of a timber species is renewed 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 3 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. 2010). 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 economically and ecologically inappropriate to manage the timber resources of these fast-growing low-density timber species.

The management of these shade-intolerant/light-demanding pioneers in young successional stages of the Amazonian floodplain forests (Salo et al. 1986; Terborgh

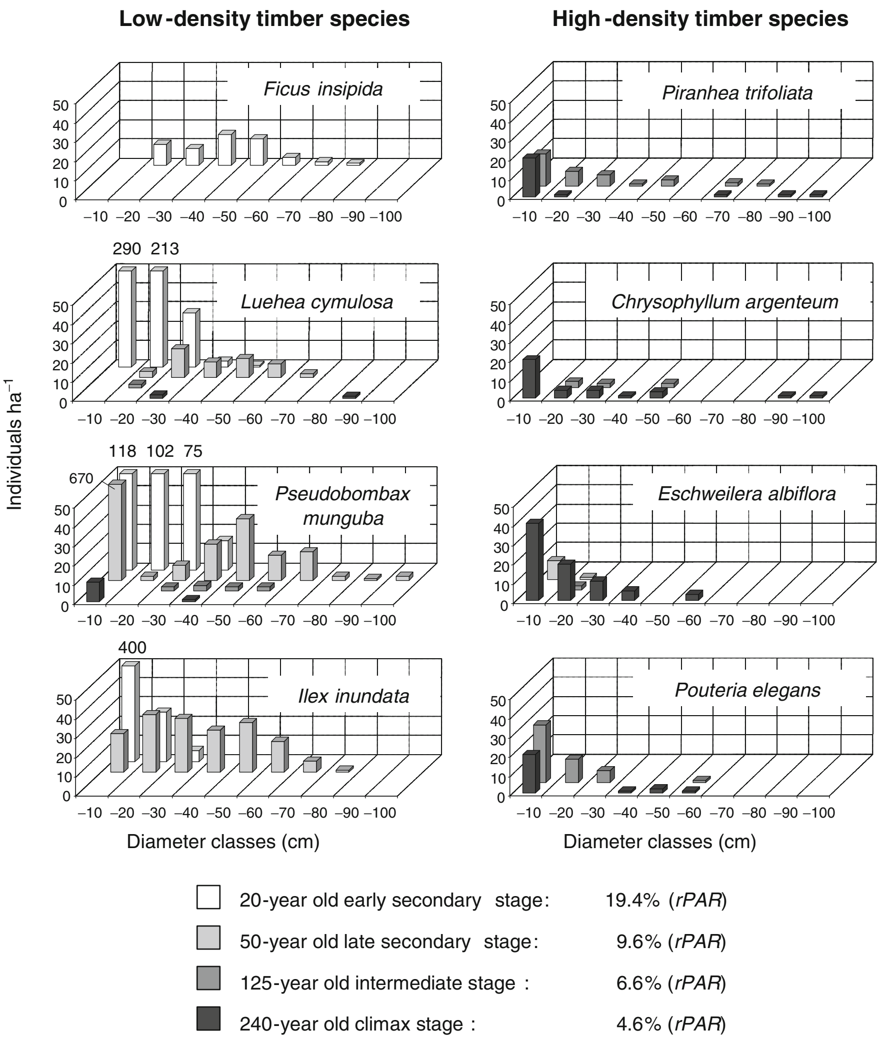


Fig. 21.11 Population structure (abundance for 10-cm diameter classes) of the low-density timber species (*left*) and high-density timber species (*right*) of four different successional stages (Schöngart 2008). Data for mean, minimum and maximum relative photosynthetically active radiation (*rPAR*)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

et al. 1997; Wittmann et al. 2004) requires a monocyclic silvicultural system (Shelterwood Systems) (Lamprecht 1989; Dawkins and Philip 1998; Whitmore 1993) (Fig. 21.12). Monocyclic systems support a uniform crop of trees from the young regeneration phase and allow both heavy harvesting and broad silvicultural treatments. A new even-aged crop is established by applying preparatory and establishment cuttings to achieve natural regeneration (i.e., seedlings and saplings) of the desired trees. At an appropriate time, the overstorey of all marketable stems

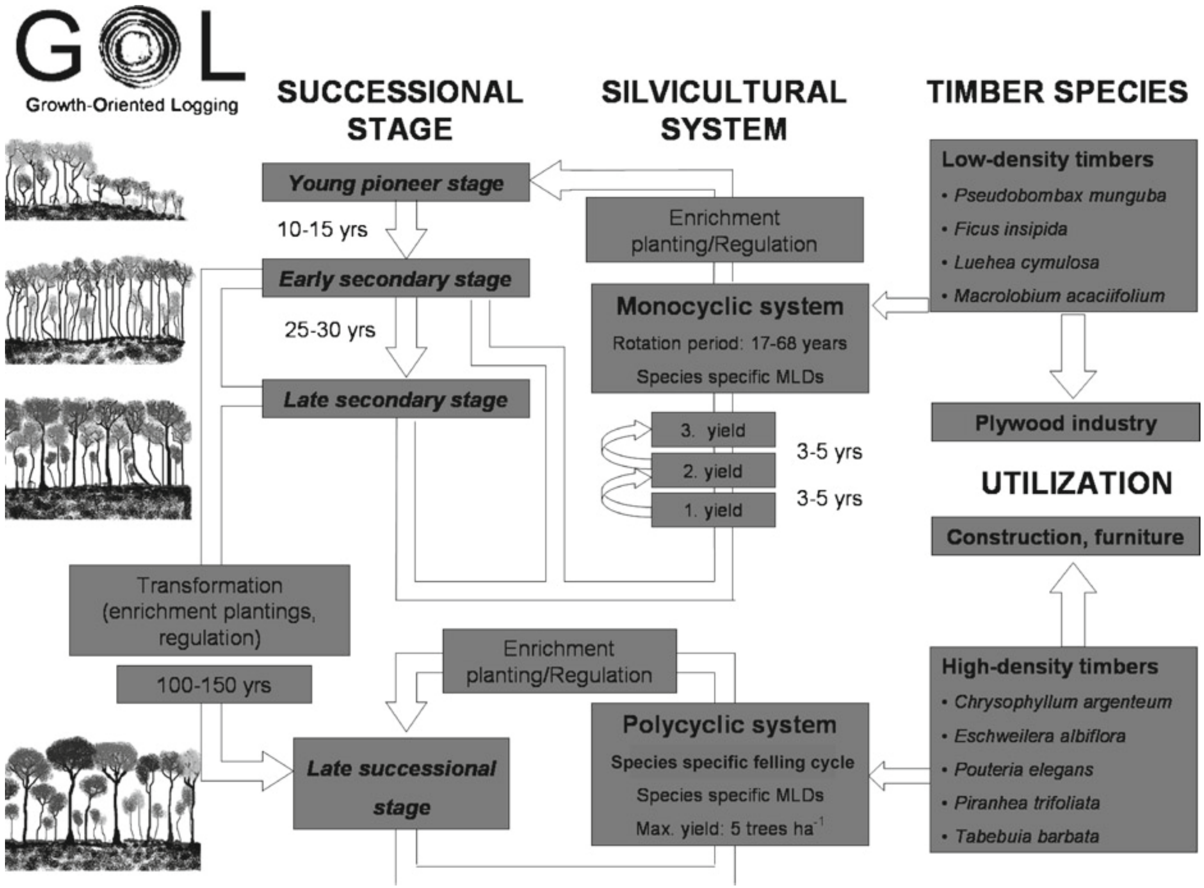


Fig. 21.12 Forest management concept for Central Amazonian floodplain forests of the low várzea, differentiated for low-density (monocyclic system) and high-density (polycyclic system) tree species (Schöngart 2008)

is removed in one or more harvestings. The period between the establishment of the seedlings and the harvest of the mature trees is defined as the rotation period (in contrast to the felling cycle). The advantage of this system is the high economic efficiency and immediate cash flow, but problems arise in terms of nutrient removal, the risks of soil erosion and the need for often intensive silvicultural work, such as beating-up or weeding/cleaning, and later tending and thinning (Lamprecht 1989; Bruenig 1996). A well known monocyclic system is, for instance, the Malaysian Uniform System which became introduced in lowland dipterocarp forests in 1948 by Wyatt-Smith (1963). It consists of felling the mature crop of all trees above 45 cm diameter, poison girdling all defective relics and non-commercial species down to 5 cm diameter and releasing established seedlings.

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

Another option is to transform stands of the early forest succession, either directly or after one or more rotation periods, into intermediate and climax stages made up of high-density timber species. This corresponds to the natural succession dynamics of low-várzea forests (Salo et al. 1986; Terborgh and Petren 1991; Worbes et al. 1992; Wittmann et al. 2002b; Wittmann et al. 2010). As forest succession (primary succession) initiates on newly created areas by the sedimentation processes of white-water rivers, the newly established areas compensate for those transformed to late successional forests. Silvicultural treatments such as enrichment plantings and regulation of the natural forest regeneration of occurring timber species may be viable, but costly options which need further research. Also, in a later step, the pruning of selected future crop trees might by a silvicultural 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. 2010a). 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-aged structure (Worbes et al. 1992; Schöngart et al. 2003). This species group achieves timber stocks of 57–70 m^3 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 2010). 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 at an age of 60–90 years, while current volume increments reach their maximum in trees at an age of 160–230 years (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 some high-density woods in the várzea are over-exploited, as is the case for *P. trifoliata*, which dominates late successional stages in low-várzea forests (Worbes et al. 1992). In a late successional stage, 29 trees >10 cm diameter were recorded in a 1-ha plot (Schöngart 2003). A simulation of selective harvesting under current management options, as practised in the MSDR (Schöngart and Queiroz 2010), produced a yield of 9.2 m^3 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 recuperation of the initially harvested volume (9.2 m^3 ha^{-1}), and a stem volume of only 3.1 m^3 ha^{-1} could be forecasted for the next harvest ($n=3$ trees). To achieve a sustainable yield of *P. trifoliata* under current management options, a felling cycle of 60 years needs to be applied, which makes forest management for this tree species economically unviable. Predictions of in-growth for one felling cycle still need improvement, including

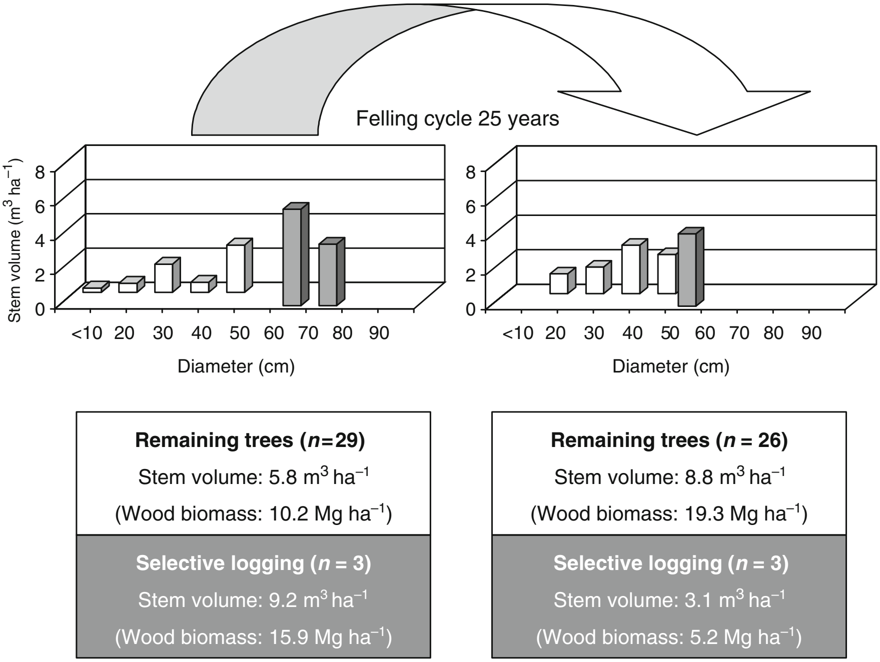


Fig. 21.13 Simulation of selective logging (polycyclic system) of the high-density timber species *Piranhea trifoliata* in a mature low-várzea forest under currently practised forest management criteria (felling cycle of 25 years; diameter cutting limit of 50 cm). Data on population structure and stem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

information on the species-specific mortality rates in different diameter classes, recruitment rates, and the reactions of the residual trees after selective logging, which are monitored in permanent sample plots. However, the prospective analysis (Fig. 21.13) clearly indicated that current management practises are unsustainable and lead in the specific case to an overlogging of the timber stocks of *P. trifoliata* because the potentially most vigorous trees are removed before they reach their optimum volume growth. The IN n° 5 enables also a management option in the várzea with felling cycles of 10 years and a low periodic yield of 10 m^3 ha^{-1} of commercial volume (MLD >50 cm) restricted to 3 trees ha^{-1} independent from the tree species. It is obvious that a management adopting these measures would lead to a dramatic decline of the timber stocks of *P. trifoliata* with probably also negative effects on genetic diversity and demographic structures of the species. The increase of the DCL 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 ± 0.07 g cm^{-3}) than obtained in old-growth forests made up of stands of trees over 200 years old (0.84 ± 0.10 g cm^{-3}) (Fig. 18.5 in Schöngart et al. 2010). 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 3 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 and Queiroz 2010).

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

Other studies have evaluated stand growth and development for a period of 240–400 years by using process-oriented forest growth models, for example, for Southeast Asian dipterocarp lowland forests (Huth and Ditzer 2000; Huth et al. 2005) or tropical forests in Venezuela (Kammesheidt et al. 2001). These models are based on carbon balances of individual trees from different crown layers, as determined by the main physiological processes (photosynthesis, respiration) (Bossel and Krieger 1991; Jansen and Martin 1995) and by allometric functions relating aboveground biomass, tree height, stem diameter, and crown parameters. However, estimations of maximum tree ages were based on assumptions and the effect of increasing atmospheric temperature and CO_2 concentrations (IPCC 2007) and their feedback on photosynthetic and respiration rates was not considered (Cox et al. 2000). This calls into question the suitability of these models to predict stand development of dipterocarp lowland forest for the next 240–400 years (Huth and Ditzer 2000; Huth et al. 2005). These models also are not able to define species-specific management options.

In contrast to other methods of modeling 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; Worbes and Fichtler 2010).

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 2010) 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; Rosa 2008; 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).

Achieving sustainable yields requires the species- and site-specific management of timber resources (van Gardingen et al. 2006; Sebbenn et al. 2008), in which the different growth features of low- and high-density timber species and the varying site conditions are considered. The GOL concept for the low várzea (Fig. 21.12) is adapted to the natural dynamics of the successional forest and offers an approach to sustainability based on the population structures and wood increments of low-

Table 21.2 Forest management projects with polycyclic systems (selection management system) in tropical non-flooded (terra firme) and floodplain forests (adapted from Worbes et al. 2001)

Polycyclic system	Project size (ha)	Yield (m^3 ha^{-1})	Felling cycle (years)	Yield (m^3 ha^{-1} $year^{-1}$)
PT. ITCI (terra firme) Kalimantan, Indonesia	601,750	57	35	1.6
North Queensland (terra firme) Australia	160,000	20	40	0.5
TSS Nigeria (terra firme)	90,000	35	50	0.7
Celos Suriname (terra firme)	20,000	30	25	1.2
Mil Madeireira Brazil (terra firme)	>400,000	35–40	25	1.4–1.6
Gethal Brazil (terra firme)	71,000	21–151	30	2.8 (0.7–5.0)
Gethal Brazil (várzea)	43,000	37–78	30	1.7 (1.2–2.6)
MSDR, Brazil	20,000	38	25	1.2

and high-density tree species. The application of modified monocyclic systems to early forest succession and of polycyclic selection systems to old-growth forests preserves the multiple ecological functions of these forest ecosystems while at the same time supporting both the growing riverine populations and the expanding timber and plywood industries of Amazonia. Sustainable forest management in the low várzea can thus be seen as a mean to decrease the pressure on timber species populations of high-várzea sites. In contrast to high-várzea forests, low-várzea forests have a large proportion of endemic tree species (Wittmann et al. 2010) and are characterized by their high floristic similarity over large geographic distances due to long-distance dispersal by currents and fishes (Wittmann et al. 2006a). Concepts like the one formulated by GOL offer a powerful tool to promote the sustainable forest management of timber resources not only for other forest ecosystems in Amazonia but also for other tropical regions.

Nevertheless, felling cycles or rotation periods only guarantee the sustainable use of timber resources if the harvested species recruit. Little information is available on the germination, growth, and establishment of seedlings and saplings or their relation to external abiotic (flooding, light conditions, water and nutrient supply) and biotic factors (seed banks, inter-specific and intra-specific competition, herbivory) (Oliveira Wittmann et al. 2010). Costs-benefit analyses are necessary to evaluate silvicultural improvements, such as enrichment plantings, thinning to regulate recruitment and competition, as well as the pruning to increase stem qualities (Lamprecht 1989; Mesquita 2000). This would promote development of an appropriate silvicultural strategy – one that is based on scientific data – to increase the sustainability of tropical forests. Future studies should test the concepts formulated by GOL against conventional management systems (IN n°5) and unmanaged forests (control) focusing on the population dynamics of timber species. Immediate efforts is crucial to obtain realistic estimations of tree ages, increment rates, volume production, population structure and regeneration processes of commercial tree species growing under varying edaphic, hydrologic, and climatic conditions. The participation of the riverine population in this phase is essential to analyse the time and cost demands in the different activities (forest inventure, logging, skidding, etc.) and calculate the income (wood quality, wood prices). This allows performing cost-benefit analyses which are a powerful tool to evaluate social and economic aspects of the sustainablity of different management options. Public policies, represented by the IBAMA, Institute of Environmental Protection of the Amazonas State (IPAAM) and Secretary for Environment and Sustainable Development of the Amazonas State (SDS) and other stakeholders such as NGOs, municipalities and timber industries should participate from the beginning to monitor and validate new management concepts. This increases the possibility of a step-wise implementation of adaptive management in paractise and forest legislation to rationally approach sustainable management and conservation. This guarantees the welfare of the involved local populations and maintains the ecosystem's multiple services and is a long-term ecological and socio-economic viability of the management of timber resources in the central Amazonian várzea floodplains.

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Part IV
Discussion and conclusions

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

Helder Lima de Queiroz and Nelissa Peralta

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Abstract "The importance of protected areas, among the many existing strategies of Amazonian várzea conservation, is discussed in this chapter through the case of the Sustainable Development Reserve (SDR), a recent category of protected area created and tested in Brazil during the last 15 years. The case of Mamirauá Sustainable Development Reserve (MSDR), the first of its kind, is presented in detail to serve as a valid description the model. This new form of management of a protected area developed at Mamirauá was successful because it not only provided improved levels of protection to local biodiversity, but also builds an important alliance with the traditional inhabitants of the area. This case suggests that protected areas of sustainable use can be viable tools for the protection and conservation of várzea environments in Brazil. As a highly populated ecosystem, these flooded forests are under intense human pressure. Although effective protection in strategic portions of flooded areas would be vital for recovery of most stocks of natural resources, it is nonetheless very difficult to create and implement protected areas with the absence of humans in várzea. Protected areas involving locals seem to be a more viable solution to the challenge. The conservation of this ecosystem also demands important action beyond the protected areas strategy. However, any large scale strategy for Amazonian conservation necessarily call for involvement and

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participation of local traditional populations. This is particularly relevant in respect of várzea conservation. In consequence, social factors must be always considered in the process of conservation planning of várzeas in Brazil. "

22.1 Introduction

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

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

22.2 Localization of the Area

The MSDR is located at the confluence of the Solimões and Japurá Rivers and the Auatí-Paranã, a branch of the Solimões draining into the middle course of the Japurá (Fig. 22.1). Mean water level fluctuations in the MSDR are about 11.4 m (Schöngart

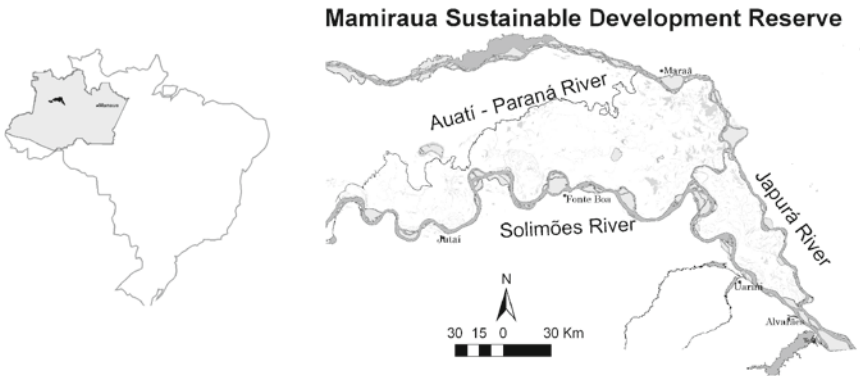

Fig. 22.1 Localization of Mamirauá Sustainable Development Reserve in Brazil

et al. 2005). When floodwaters are at their highest point, virtually all lands of MSDR, or 1,124,000 ha, are completely submerged, and only the highest parts of the forest canopy can be seen above the water line (Sociedade Civil Mamirauá 1996). The flood pulse is mono-modal, with high predictability and high amplitude (Junk 1997b). It defines the whole biology of the aquatic terrestrial transition zone, which is mostly covered by different types of floodplain forest (Wittmann et al. 2002b).

The MSDR is the largest Brazilian protected area devoted to the conservation of the biodiversity of floodplain forests, and one of the few functional protected areas conserving the várzea forests in Brazil. Other reserves protecting várzea are Piagaçu-Purus Sustainable Development Reserve, Resex (*Reserva Extrativista)* Auatí-Paraná, Resex Unini, and Jutaí-Solimões Ecological Station.

22.3 Biodiversity in the MSDR

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

Differences in the elevation of terrain, and consequently, the duration of flooding, lead to the development of distinct terrestrial habitats during the low water season, with different vegetation structures and compositions in the várzea ecosystem (Ayres 1993). According to the protected area's management plan, about 10.2% of the area is covered by permanent water bodies, and out of the remaining 89.8%, 44.3% comprises low and high *restingas* (flooded forests located in higher levees), 31.3% is made of *chavascal* (flooded shrubby vegetation located in lower areas, Wittmann et al. 2010), and 14.2% is formed by other plant communities (palm groves, grasslands, beaches and cleared lands and gardens) (Sociedade Civil

Mamirauá 1996). Other habitat classifications have been put forward, Wittmann et al. (2002b), for example created a new classification system for vegetation in várzeas based on aerial photography and satellite imaginary, describing two main habitats – low and high várzeas (Wittmann et al. 2010).

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

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

To date, about 340 fish species have been recorded in the MSDR and in the immediately adjacent bodies of water. There is little doubt that Mamirauá has an exceptionally diverse fish fauna. This is the greatest number of species ever registered for a várzea environment. The reason for this diversity is probably the range of aquatic habitats available and the wide environmental fluctuations that characterize the hydrologic regime (Queiroz and Crampton 1999).

22.4 History of Human Occupation and Use of Natural Resources in Mamirauá

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

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

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

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

22.5 The Sustainable Development Reserve Model

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

The impact of this new category of protected area in Brazil was considerable, and Márcio Ayres, his group and their proposals had a very positive impact in the National System of Protected Areas (SNUC). This system, approved by the

Brazilian Congress in 2000, brought to the Federal level the category of SDR. Nowadays this category is well distributed in the Amazon, and also in other Biomes, such as the Atlantic Forest (*Mata Atlântica*).

22.5.1 Participatory Management

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

Before the transformation of the Ecological Station into SDR, an ample array of scientific studies was produced in order to serve as a base for the elaboration of the management plan (Queiroz 2005a). This research program lasted for three years, minimum amount of time considered necessary to obtain sufficient information for the first management plan proposal, which was discussed with the local population throughout 1995 and finally approved by the government in 1996. Scientific research programs in the reserve continue and some of the results are referred to in different chapters of this book (e.g., Wittmann et al. 2010; Oliveira Wittmann et al. 2010; Schöngart and Queiroz 2010).

The sustainable development model is implemented through the creation and approval of norms and regulations for the use of natural resources, including the zoning system. This zoning system, with its norms and regulations, was a result of a long process involving the population in its elaboration and negotiation, and culminating 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.

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

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

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

Different levels and forums of discussion allow for legitimating and appropriation of decisions, and enhance local population's ability to control and manage their own resources. Disputes and conflicts that arise due to the existence of many different intra and inter community interests are dealt with in other forums like sector meetings, general assembly, and ultimately in the deliberative council.

Involvement and participation are also important in other levels. There is always the need for accordance or approval by the local representatives for any activity carried out in the areas of a particular village or group of villages. Scientific research, visitation, guarding, and management in itself have to be approved by locals or their representatives, who also are directly involved in those activities. This system of involvement and participation, together with a continued service of environmental education and circulation of relevant information, grant the improvement of representatives through time, the high quality of discussions and deliberation, and a good level of commitment of local population with conservation of the protected areas (Queiroz 2005b; Queiroz and 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 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 people, but their use must be regulated by the norms of the management plan. In addition to these two main zones, there are also special management zones, areas where the use of a specific resource has to be regulated (Sociedade Civil Mamirauá 1996).

22.5.3 Norms for the Use of Natural Resources

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 2010; Schöngart and Queiroz 2010). Studies on hunting and agriculture, which were

Fig. 22.2 Zoning System for the focal area of Mamirauá Sustainable Development Reserve

more related to the use of species, were also fundamental for understanding the spheres of action of local communities (Sociedade Civil Mamirauá 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

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

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

Natural resource management programs in Mamirauá act in three different spheres: At the economic sphere, with generation of income; at the sociopolitical sphere, by creating systems of natural resource management that integrate access to resources with participation of locals in its protection; and at the ecological sphere, aiming to promote better conservation levels for renewable natural resources.

The implemented natural resources management systems were developed from traditional practices allied to low impact techniques based on scientific research. A monitoring system was built and is used in order to evaluate effectiveness of management models and practices. In some cases, these economic alternatives represent the adaptation or re-structure of traditional activities, such as fishing, timber exploitation, and agriculture. In other cases, new economic activities are introduced like ecotourism (Peralta 2005) and exploitation of non-wood forest products (NWFPs) (Wittmann and Oliveira Wittmann 2010).

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

Another example of this effect was produced by those communities and associations involved in the development of ecotourism inside Mamirauá. The profits 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 below the minimum size of catch established at the time by the IBAMA, which is 150 cm of total length. This evidence of bad traditional management and its consequences was crucial to draw the attention of local social actors, especially the fishermen inside the reserve, and led the way to the agreements about new regulations and modifications in the behavior of local fishermen. The need for large-scale change was evident, and the best way to promote this was engaging local social actors in management of resources. Promoting best practices of sustainable use in pilot management systems was an idea that followed the publication of Mamirauá Reserve Management Plan, in 1995/96. Consequently, in 1998, after a series of initial studies (Queiroz 1997; Queiroz and Sardinha 1999; Queiroz 2000) added by further studies (Castello 2004, 2007; Viana et al. 2004), the most important pilots of management systems were put in place. In that year, the promotion of sustainable fisheries of *pirarucus* started.

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

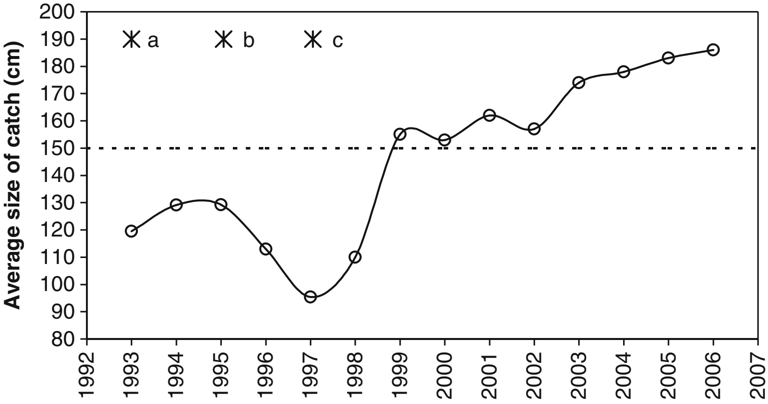

Fig. 22.3 Average size (total length in cm) of *pirarucus* caught from 1993 to 2006 at Jarauá sector, MSDR, represented by the open circles. The dotted line represents the minimum catch size of the specimen established in the current legislation. Marks represent important moments in the management history.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

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

Something similar happened to the management system of timber (Pires et al. 2001). As it is largely recognized, illegal logging in the Amazonian várzeas is one of the most important threats to these forests, since more than 60% of the timber exploited by the industry in the region comes from várzeas (Klenke and Ohly 1993; Higuchi et al. 1994; Schöngart and Queiroz 2010). Even after a program of awareness and environmental education (focusing also on loggers) was put into place in 1993, illegal logging continued in Mamirauá (Albernaz and Ayres 1999). Despite local producers and local communities agreement on the need to stop unsustainable exploitation of timber (including threatened or rare species), it was only when the productive management of logging started, two years afterwards (in 1998) that illegal timber extraction was really reduced inside the protected area (Fig. 22.4).

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

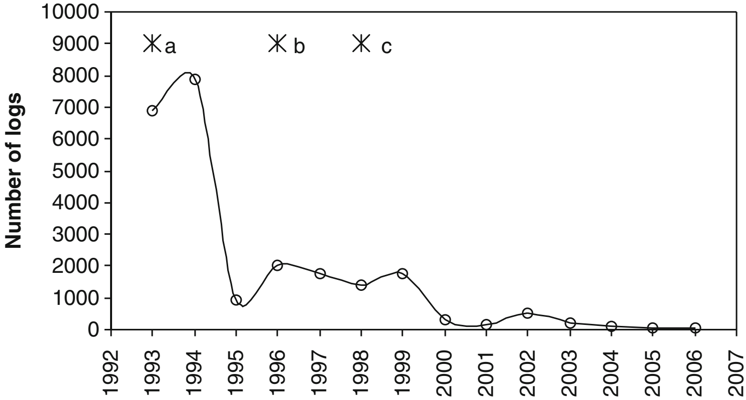

Fig. 22.4 Number of logs removed from MSDR between 1993 and 2006. Marks represent important moments in the timber management history. **a**: In 1993 starts the campaign of public awareness and environmental education in regard of illegal timber extraction. **b**: In 1996 the management plan was published 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 subside 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. 2010). 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 2010; Schöngart et al. 2010). 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 50 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 2010; Schöngart and Queiroz 2010).

22.6 Improvements in the Quality of Life

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

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

Despite the fact that "quality of life" can be measured by different indicators, the improvement in income generation has impacted many other aspects of social life, like health and education of the villages inside Mamirauá. Although the increase in income generation is considerable, the other social, cultural, political and economic indicators were also important sources of attraction towards the management systems for all the marginal communities around Mamirauá. Maybe one of the more important impacts of the improvement in income of locals in the reserve (as a consequence of productive management of natural resources) is that infant mortality was reduced almost four times during the last 15 years (Fig. 22.6). Infant mortality is here measured as the number of one year old infants, or younger, deceased for

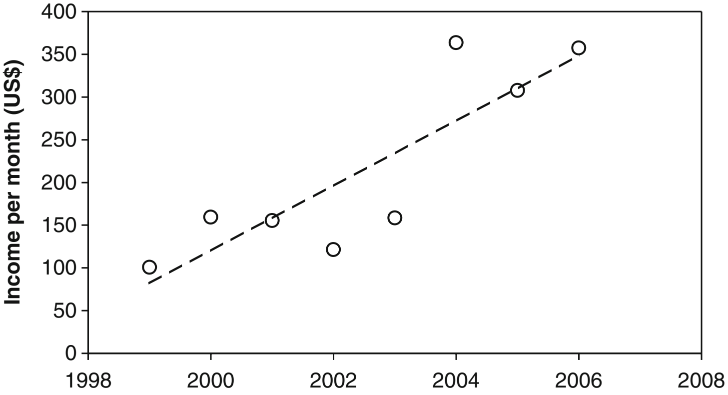

Fig. 22.5 Income (in US$) per capita per month of fishermen involved in the management systems of *pirarucu* fisheries at Mamirauá, from 1999 to 2006 (with data modified from Viana et al. 2007)

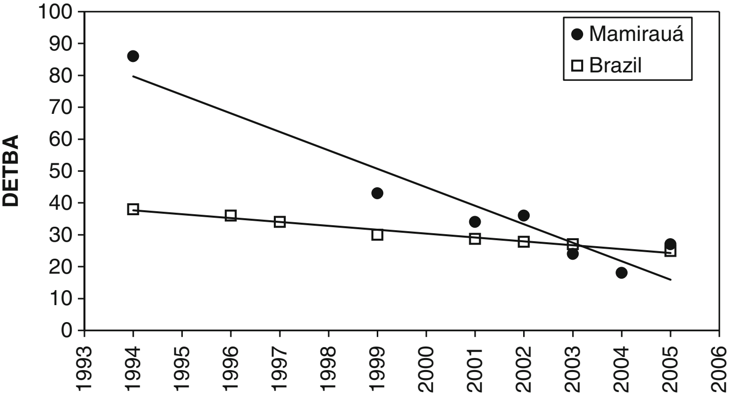

Fig. 22.6 Infant mortality at Mamirauá and in Brazil, measured as the number of deaths for each thousand born alive – DETBA

each group of thousand children born alive. During the period when this indicator was monitored, there was a yearly 20% decrease.

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

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

Clearly, the legal framework to support sustainable use of natural resources inside protected areas, and participatory management of natural resources as a whole need more clarification and regulation by the Brazilian authorities. Perhaps most of the problems identified so far, and briefly described above, could benefit from clear official regulation. In addition to that, availability of strong and comprehensive data on the biology of the natural resources to be exploited, as well as information on social and economic aspects of management is crucial to the success of the system implemented. Other important aspect for in-depth research is the carrying capacity of different types of natural environments (with and without deep disturbances).

22.7 Conclusions

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

All the positive environmental and social impacts of Mamirauá described above suggest that protected areas can be viable tools for the protection and conservation of

Brazilian várzeas. Since it is a highly populated ecosystem, the Amazonian flooded forests are under intense human pressure. Depletion of natural resources tends to be followed by biodiversity losses, and finally a large and wide degradation of the physical structure of the environment. Establishing effective protection in strategic portions of flooded areas is vital for recovery of most stocks of natural resources.

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

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

Chapter 23
The Role of Floodplain Forests in an Integrated Sustainable Management Concept of the Natural Resources of the Central Amazonian Várzea

Wolfgang J. Junk, Maria T.F. Piedade, Florian Wittmann, and Jochen Schöngart

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Abstract This chapter provides an overview of the use of Amazonian floodplains and makes proposals for their sustainable management. Archaeological artifacts show that humans colonized the lower Amazon River floodplain (várzea) about 12,000 years BP. The first Europeans that traveled along the Amazon River described densely populated stretches of river shores. Soon after the arrival of the Europeans, introduced diseases, wars, and slave raids dramatically reduced the numbers of indigenous people and disintegrated their communities. Export-oriented exploitation led to the quick destruction of the large stocks of turtles, manatees, caimans and other wildlife. Today, important uses of the floodplains for fisheries, subsistence agriculture, forestry, and cattle and buffalo ranching are concentrated in the nutrient rich whitewater river floodplains. With an estimated potential of about 900,000 t yr^{-1}, inland fisheries have a large economic potential that is not yet fully exploited. Agriculture is of increasing importance near urban centers. Forestry is still restricted to selective extraction of a few timber species, depleting their stocks. Low density cattle and buffalo ranching are expanding, at a cost to forestry, because ranchers destroy the forest to increase their pasture areas. This also negatively affects fisheries and biodiversity, because forests provide food sources for many commercially important fishes and habitat for many plant and animal species. Within the floodplain, all management methods are influenced by the annual hydrological cycle and people cope well with it; however, extreme floods and droughts result in serious economic losses and threaten human life. Scientists have proposed several strategies for improving the management of floodplain resources, such as the multiple-use concept, the concept of participatory management of fishery resources, and the concept of growth-oriented logging of várzea forests. A new model for the prediction of peak floods and droughts, based on sea-surface temperatures of the Pacific and Atlantic Oceans, help people to take preventive actions. However, in practice there are still serious deficiencies in the application of scientific knowledge because of lack of cooperation between scientists, politicians, and planners. There are a few implemented projects, such as the reserves for sustainable management, but until now experiments in modern, integrated, floodplain adaptive management are still in their beginnings.

23.1 Introduction

The floodplains along the Amazon River and its large whitewater tributaries cover about 200,000 km^2, 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 1984a; 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.

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

23.2 History of Human Occupation of the Amazon River Floodplain

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

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

The first Europeans traveling along the Amazon River observed large settlements along the River's shores, with luxurious home-gardens and plentiful food. According to Denevan (1976), pre-Columbian population density in the non-flooded upland, locally called terra firme, reached about 1.2 people per square kilometer, 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 against 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).

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 Irmler (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 Piedade 2010). The low fertility of its water and sediments makes the igapó of blackwater rivers unsuitable for agriculture, cattle-ranching, and forest culture. Fish biomass is about one fifth of that of the várzea (Saint-Paul et al. 2000). The nutrient status of clearwater river floodplains is better but inferior to that of whitewater rivers (Furch 1997, 2000; Furch and Junk 1997a). Considering the high biodiversity of the igapó forest, the most suitable management of the igapó is by extensive fishery, ecotourism, and the sustainable extraction of non-timber products. Only the várzea has the economic potential to support fishery, agriculture, ranching, and forest culture.

The várzea and igapó are pulsating systems, i.e., they alternate between a terrestrial and an aquatic phase. The conceptual considerations regarding pulsating systems are described by the flood pulse concept (FPC) (Junk et al. 1989), which has been recently rediscussed and updated (Junk and Bayley 2008; Junk and Wantzen 2004; Junk 2005). The flood pulse of both the várzea and the igapó is monomodal, predictable, and of high amplitude (Fig. 23.1). This favors the adaptation of plants and animals to the change between the aquatic and the terrestrial phase and allows sufficient time for organisms to make use of the floodplain's resources. For example, fish migrate during rising and high waters into the flooded forest to feed on fruit, seeds, terrestrial insects, and terrestrial detritus but also on

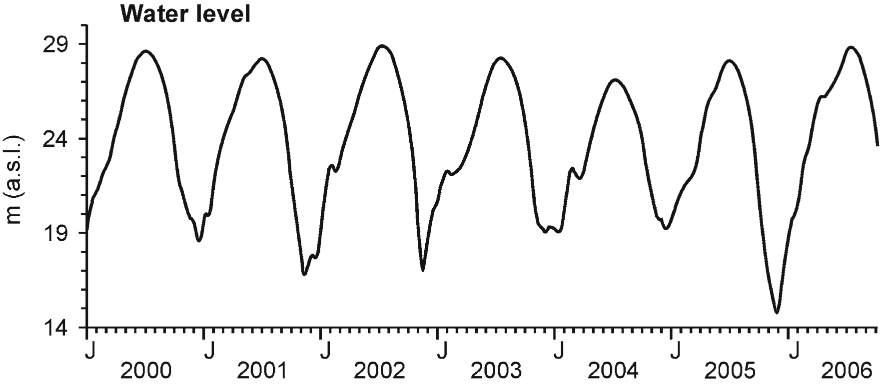

Fig. 23.1 Water-level fluctuations of the Negro River at Manaus. Data provided by the Manaus harbor authorities

phytoplankton, periphyton, aquatic macrophytes, zooplankton, and aquatic insects produced in the floodplain. At low water, fish migrate back into permanent water bodies and river channels, and terrestrial plants and animals occupy the floodplain (Fig. 23.2). There is an intense exchange of nutrients and energy between the rivers and their floodplains. Flood pulsation increases and maintains habitat and species diversity but also results in heavy losses within the plant and animal populations. Organisms react with different strategies, including high reproduction rates, rapid growth, and early maturity, to compensate for these losses. In the nutrient-rich várzea, this behavior leads to high levels of primary and secondary production, whose products can be used by humans. For details see Junk (1997a).

Its recognition of the events associated with rising and falling water levels supports the FPC's use as the scientific basis for broader concepts dealing with the sustainable management of the várzea. The multiple use concept (Junk 2000a) concludes that the high productivity of the várzea during the aquatic and terrestrial phases can be best used by recognizing the complex interactions between the two. Large-scale changes in hydrology, e.g., by dikes to prevent flooding, will negatively affect productivity and thereby change plant and animal communities. Destruction

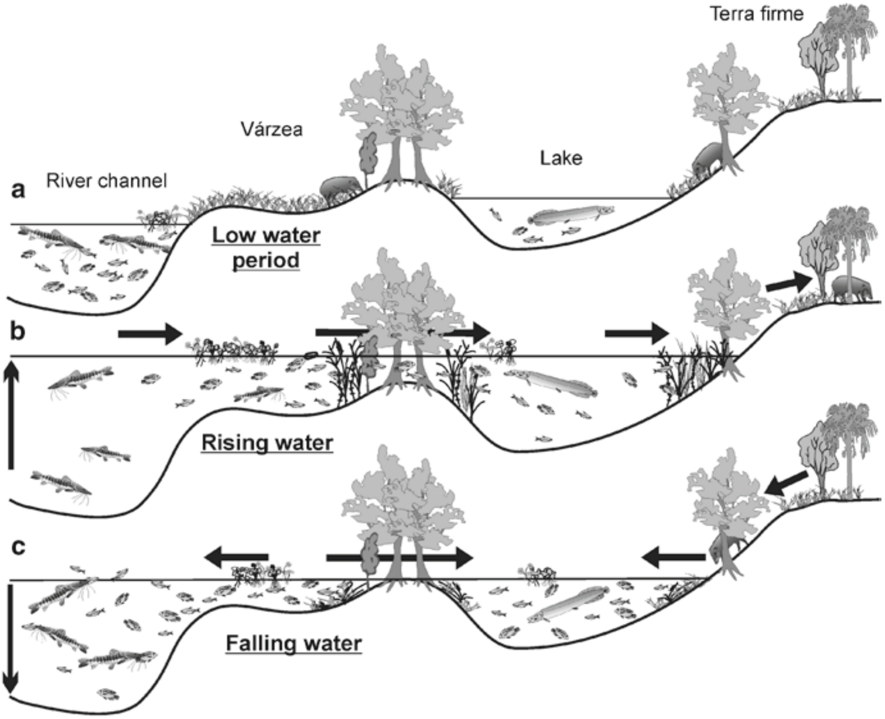

Fig. 23.2 Migrations of fish and terrestrial mammals between the river channel, floodplain lakes, floodplain, and upland at different water-level stages

of the floodplain forest reduces the availability of food for many commercially important fish species. Agrotoxics used by farmers during the dry period poison aquatic organisms, including fish and their larvae, at rising water levels. Optimization of the economic outcome of the different management options is required instead of maximization of the economic outcome of a single option, for instance by avoiding agricultural and cattle-ranching activities that may be prejudicial for fishery.

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

All activities in the várzea are related to the water level. Although the flood pulse is predictable in its timing and height, there are variations of several meters in its amplitude (Fig. 23.1). This natural variability regulates the várzea's plant and animal populations and contributes to the high biodiversity and productivity of the system (Intermediate Disturbance Hypothesis; Connell 1978). For management purposes, however, it creates serious problems. High floods destroy crops and may kill livestock; low floods inhibit the extraction of timber from the floodplain, and very low water levels hinder navigation as well as the transport of goods and result in large kills of fishes and other aquatic animals. A precise forecast of the hydrograph is essential for the riverine population to adapt their activities accordingly and to minimize losses. Since 1989, monthly forecasts of the maximum water level have been made from March to May by the Serviço Geológico do Brazil (CPRM). The hydrological models are based on statistical analyses of hydrological data sets.

Recently, a new method was proposed that may complement the CPRM forecasts (Schöngart and Junk 2007). This method incorporates the fact that rainfall in the Amazon basin is influenced by El Niño and La Niña events, which can be predicted by sea-surface temperature (SST) anomalies of the tropical Pacific Ocean. High SSTs indicate El Niño years associated with low rainfall in the Amazon basin and low flood levels, and low SSTs La Niña years, with high rainfall in the basin and high floods (Schöngart et al. 2004). SST anomalies as well as the Southern Oscillation Index (SOI) correlate well with the high-water level (Fig. 23.3). The forecasted and observed maximum water levels of the last 5 years are given in Fig. 23.4.

From 1950 to 2005 the minimum water level at the harbour of Manaus shows a significant correlation with monthly SST anomalies in the tropical North Atlantic (TNA, 05°–20° N/60°–30°W). The correlation between minimum water level and monthly SST anomalies in the TNA is evident for 11 consecutive months before the appearance of the minimum water level. Warm SSTs in the TNA are also the source of tropical cyclones and hurricanes. Thus, there is a significant relationship between the minimum water levels in Manaus and the accumulated cyclone energy (ACE) index (Trenberth 2005), since both are

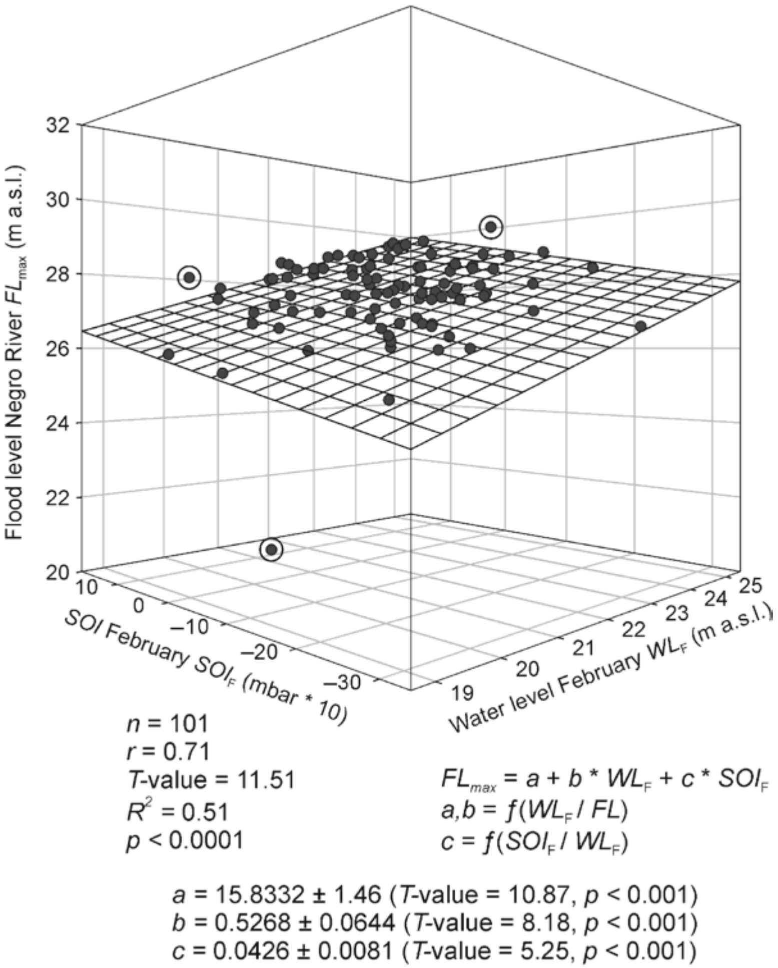

Fig. 23.3 Multiple regression model to forecast the maximum water level of the Negro River (Manaus) using the mean water level and Southern Oscillation Index (SOI) for February during the period 1903 to 2004 (101 years). The model explains 51% of the variability of the parameters; only in 3 years (3% 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

related to the increased SST in the TNA. In years in which the ACE is above normal (median >117%), the water level in Central Amazonia is in average 155 cm below the minimum water level of other years. Tropical cyclones and hurricanes probably shift large amounts of humidity from the TNA to the Caribbean Sea and Gulf of Mexico, leading to severe droughts in Amazonia (Table 23.1).

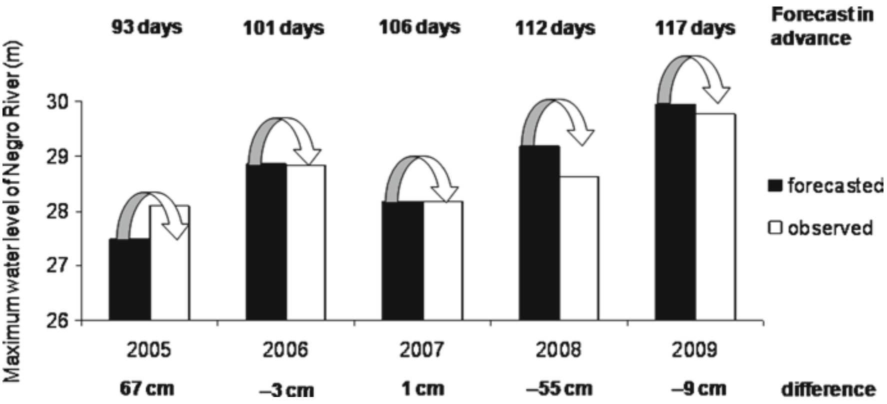

Fig. 23.4 Comparison between forecasted and observed maximum water levels of the Negro River at the port of Manaus from 2005 to 2009. The time span and difference between forecast and occurrence of the maximum water level are indicated

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

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

23.5 The Potential of Fisheries and Fish Culture

23.5.1 Fisheries

Inland fishery plays an essential role in providing high-quality animal protein at relatively low cost to the population. Estimates of the mean amount of fish consumed by rural floodplain communities vary between 370 g day^{-1} (Cerdeira et al. 1997) and 400–800 g day^{-1} (Batista et al. 1998; Fabré and Alonso 1998) and by urban populations between 50 and 194 g day^{-1} (Shrimpton et al. 1979; Smith 1979; Santos 1986/87). The Amazon basin has an inland fishery potential of about 900,000 t year^{-1} (Bayley and Petrere 1989), with inland fishery production recently estimated to be 425,000 t (Bayley 1998). Of this amount, 79% is consumed in Brazil and 20% in Peru. These numbers indicate that the fishery potential of Amazonia is not fully exploited. More than half of the catch is captured by artisanal fishermen and riverine communities for their own consumption. About 20% of the Amazonian population lives in the várzea. The easy access to fish, fruit, and carbohydrates avoids nutritional deficiencies. A portion of the region's production is sold either at small local markets or to professional fishermen and shipowners, who bring the fish to urban centers. While about 200 species are captured, only 6–12 species make up more than 80% of what is sold at the markets of major cities (Barthem and Fabré 2004).

In the 1970s, an increasing number of fishing boats together with inadequate fishery legislation led to conflicts between riverine communities and professional fishermen, which, in Brazil, could not be resolved by centralized fishery management. Therefore, by the early 1990s, the Federal Brazilian Environmental Agency (IBAMA) opted to decentralize participative management of the fishery (Fisher et al. 1992; McGrath et al. 1994, 1999; IBAMA 1994, 1997; Ruffino 1996; Isaac et al. 1998), transferring some of the responsibilities and rights to local communities, which assisted in controlling the lakes in their territories and were granted fishing rights in some of the lakes. The fish caught in those lakes can be used for local consumption or sold to professional fishermen (*reserva de lagos, acordos de pesca*). As a result of these benefits, communities began to protect their lakes. The overall impact of this approach on the local fish stocks and the fishery has not been evaluated yet; however, positive results are expected for the stocks of sedentary 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; Queiroz & Peralta this 2010). In a multispecies 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, Oreochromus 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 ha^{-1} $year^{-1}$. 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 they may escape into nature and establish viable populations that compete with natural ones, or that they will cross-breed with specimen from natural populations, thus diminishing genetic diversity. Thus, hybrid cultivation in Amazonian fish culture requires intensive research aimed at avoiding these problems, e.g., by the production of mono-sex hybrids or triploids.

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

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

23.6 The Role of Agriculture

Agriculture has economic potential only in the várzea, because of its relatively high soil fertility and the renewal of nutrients during floods. The area of the várzea, including lakes and river channels, is estimated to be about 200,000 km^2 (Junk 1997b). However, only about 5% is suitable for agriculture because these plots fulfill the following conditions. (1) They are situated along river channels and lake shores

with permanent connections to the main river channel, allowing the transport of agricultural products by boat to markets. (2) They are out of the water at least for 9 months in average per year, which provides sufficient time for planting; this area corresponds to the *várzea alta* (Wittmann et al. 2010). While watermelons and certain types of beans (*feijão de praia*) need less cultivation time, farmers cannot rely solely on these crops. (3) They are close to urban centers that offer markets for the products. The different production systems have been analyzed by several authors (Oliveira et al. 2000; Gutjahr 2000; Bueno et al. 2000; Hund and Ohly 2000; Noda et al. 2000; Lima and Saragoussi 2000; Junk et al. 2000b).
The major problems of agriculture in the várzea can be summarized as follows.

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.
2. When the river rises quickly, farmers may lose a portion of their crops.
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.
4. The concentration of production within a specific period may result in an excess of products at the market and thus to a decrease in prices.
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.
6. There are severe deficits in infrastructure, such as transport, schools, hospitals, and a reliable supply of electricity.
7. There are periods of heavy insect molestation, e.g., mosquitoes, and horseflies.

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).

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

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

		Land productivity	**Labor productiviy**	**Gross farm income**
		US$ ha^{-1}	**US$ man^{-1} day^{-1}**	**US$ $year^{-1}$**
Arable farming[a]				
Staple-crop farming		424	2.32	1,781
Vegetable farming:	Low income	468	2.24	1,639
(mixed farming)	Medium income	883	4.59	3,890
	High income	1,130	7.62	6,890
Vegetables				
(intensive)	Tomatoes	1,680	16.80	
	Cucumber	1,300	12.20	
	Lettuce	3,050	19.20	
Fruits				
	Papaya	1,896	8.50	
	Passionfruit	1,846	8.00	
	Banana	916	8.00	
Other field crops				
	Watermelon	430	16.00	
	Jute	480	1.80	
Animal farming[a]				
Cattle-ranching				
(extensive)	Beef	33.8	4.90	
	Cheese	30.6	5.56	
(intensive)	Milk	59.7	6.97	
Water-buffalo ranching				
(extensive)	Meat	32.9	11.25	
Forestry[c]				
Selective logging		15 – 57[e]		
Forest culture[c]		79 – 237[e]		
Fishery[d]				
Actual		338		
Potential		675		

[a] Junk et al. 2000b

[b] Gutjahr 1996

[c] Details in Table 23.3

[d] Theoretical production of comestible fish 90 g m^{-2} $year^{-1}$ (Bayley 1983) with a market value of US$ 1 kg^{-1}; present use: 50% (Junk et al. 2000b). Cost for fishing effort: 25%.

[e] Based on an exchange rate of 1 US$ = 1.80 BR$

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

An over-reliance on specific crops can negatively affect biodiversity in the várzea. For example, in the middle of the last century, large areas were deforested for the cultivation of the fiber crops jute (*Corchorus capsularis* L. [Tiliaceae]) and, to a lesser extent, mallow (*Urena lobata* L. [Malvaceae]) (Homma 1998). When the boom ended, in the 1980s, these areas were abandoned and subsequently became colonized first by large perennial grasses (*Echinochloa polystachya, Paspalum fasciculatum*) and later by a species-poor secondary forest that today represents the main forest cover of the lower Amazon várzea. This experience supports the need to protect at least part of the várzea alta because of its importance for biodiversity (see below).

23.7 The Impact of Cattle- and Buffalo-Ranching

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

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

The major problems of cattle-ranching can be summarized as follows:

1. Periodicity in the supply of pasture.
2. The risks of losses during high-water periods.
3. The lack of an efficient veterinary system.
4. Extensive production systems with low productivity.
5. Competition for space with agriculture and forestry and, thus, negative impacts on fish stocks.
6. Negative impacts on biodiversity because of large-scale destruction of the floodplain forest.

Despite these problems, animal-ranching in the várzea continues to increase because the demand for meat is high and the price for the producer is stable and attractive. Land productivity is low, but land is relatively inexpensive and animal production needs a small labor force. This development will increase conflicts with other stakeholders, mainly small landholders and subsistence farmers.

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

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

23.8 The Potential of Forestry

If we define forestry as the sustainable management of a forest for timber production, forestry in the várzea is in its infancy. The classic home-gardens of the riverine population can be considered traditional agroforestry systems (Lima and Saragoussi 2000; Santos et al. 2004). Preliminary experiments with *Schizolobium amazonicum*

(*Paricarana*) for plywood and cellulose production are ongoing in eastern Amazonia. Timber extraction by an expanding timber and plywood industry is of great economic importance (Higuchi et al. 1994; Uhl et al. 1998). Compared with non-flooded forests, the costs of selective logging, skidding, and timber transport in várzea forests are low because the timber is removed by boats and shipped to sawmills during the aquatic phases (Barros and Uhl 1995). Thus, between 60% and 90% of the local and regional markets in the western Amazon basin are still provided with timber from the várzea (Kvist and Nebel 2001; Worbes et al. 2001). From about 900 tree species (Wittmann et al. 2006a), only slightly more than 40 timber species are used (Parolin 2000; Kvist et al. 2001; Worbes et al. 2001). Species with low wood densities (0.20–0.60 g cm^{-3}) have mainly been commercialized for plywood production while those with high wood densities (0.60–1.00 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* (Schöngart and Queiroz 2010). 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 dendrochronological 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 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. Sustainable management of tropical forests requires data on species- and site-specific growth rates, tree age, and regeneration processes. To achieve a higher level of sustainability, Schöngart (2008) developed a management concept based on the timber stocks and growth rates of the different successional stages in the várzea. This Growth-Oriented Logging (GOL) concept is adapted to the forest's natural successional dynamics and allows for a higher degree of sustainability in tropical forest management, considering both the population structure and the wood increments of low- and high-density tree species. The development of similar concepts will provide a powerful tool to promote sustainable management of timber resources in other forest ecosystems in Amazonia and in other tropical regions.

The sustainable use of timber stocks in the nutrient-poor igapó is, under the current management options, not practicable due to the low increment rates of its tree

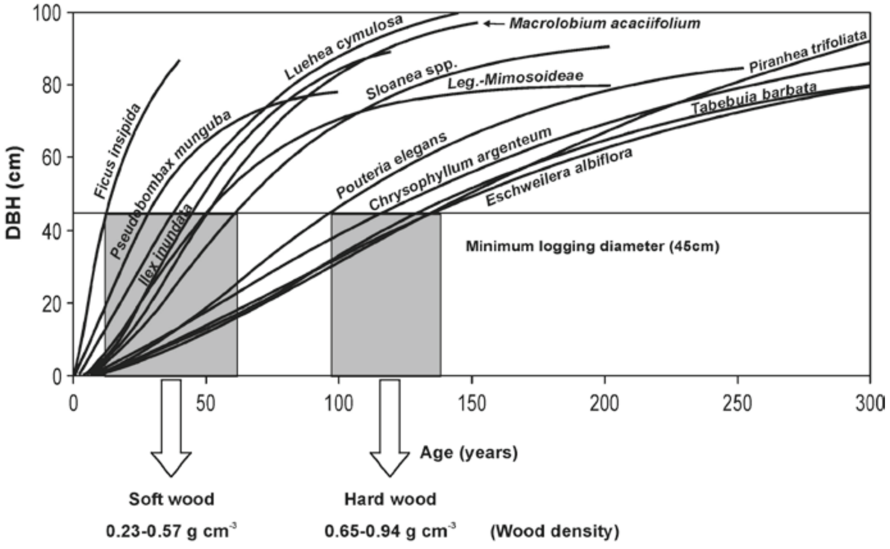

Fig. 23.5 Growth curves showing the mean cumulative diameters of 12 timber species of várzea forests. The trees are classified as low-and high-density species (Schöngart 2003). The minimum logging diameter (MLD) of 45 cm is indicated

species (Schöngart et al. 2005; Stadtler 2007; Fonseca Júnior et al. 2009). Therefore, floodplain forests of the igapó should be excluded from forest management and, instead, permanently protected.

23.9 The Impact of Different Management Options on Biodiversity

The maintenance of biodiversity is a subject of worldwide interest and is becoming increasingly important in Brazilian politics. Floodplains are of specific importance 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. 2010), 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). Flood-adapted ecotypes increase genetic diversity (Ferreira et al. 2010).

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 over long stretches of Amazonian rivers, as described by Goulding et al. (1988) for fish of the Negro River and as observed by Junk and Piedade (1997) for aquatic macrophytes. Changes occur only when environmental conditions change, e.g., a decrease in the flood amplitude at the lower Amazon River increases the number of aquatic macrophyte species rooted in the sediment and the number of bivalves

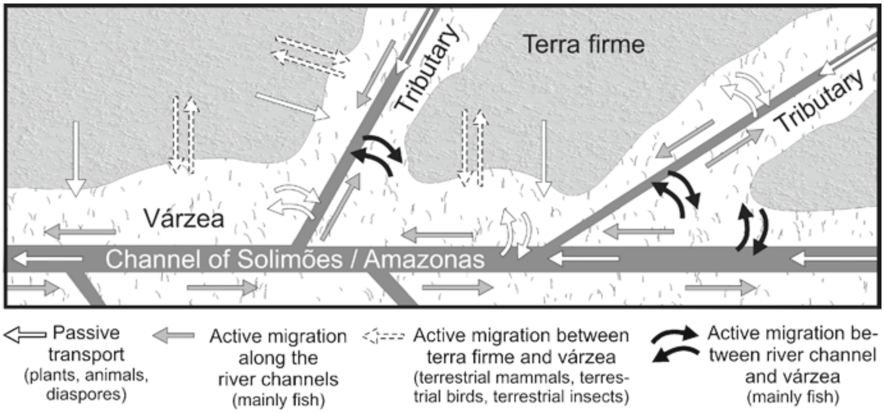

Fig. 23.6 Migration pathways and dispersal routes of organisms along the Amazon River system and between the rivers, their floodplains and the upland

that can colonize the lake sediments because of a sufficient oxygen supply (Junk, W.J. 1977, personal observation).

There is also a lateral immigration of terrestrial organisms from the adjacent upland, as shown by Wittmann et al. (2010) for trees of the floodplain forest. Despite the high and prolonged inundations, várzea forests are the most species-rich floodplain forests worldwide. The composition of tree species varies considerably along the river course at the high várzea – which is flooded to a height of only up to 3 m, corresponding to less than 50 days year^{-1} – because many species from the adjacent upland that have slightly flood-tolerant ecotypes colonize these areas. Approximately one-third of the 900 tree species recorded in várzea forests across the Amazon basin also occur in upland forests (Wittmann et al. 2006a). Of the tree species common to both ecosystems, approximately 70% are restricted to the high várzea. In várzea forests, these species show comparatively low abundances, but they increase species diversity within the high várzea exponentially. By contrast, low-várzea forests (mean inundation > 3 m in height) are less diverse, and species similarity can be high over large spatial distances (Fig. 23.7). The dominance of widely distributed low-várzea tree species is explained by the longitudinal connectivity of forest communities via seed dispersal by the rivers. Moreover, it reflects the selection pressure in response to the exceptional environmental conditions in highly flooded sites, which lead to a restricted number of highly flood-tolerant tree species.

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

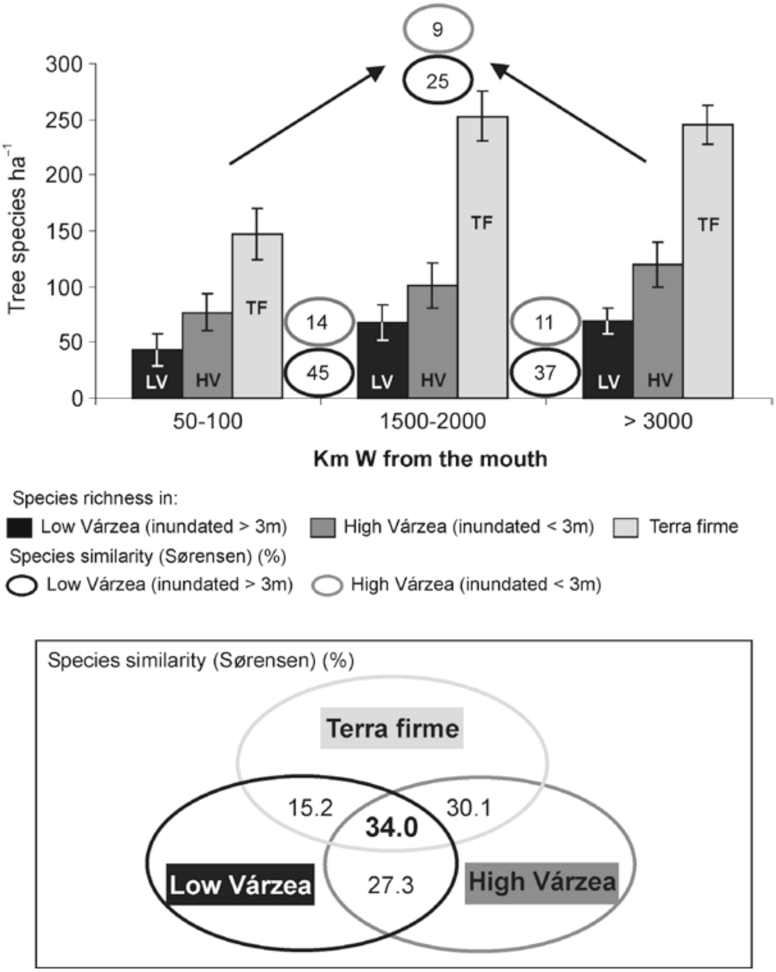

Fig. 23.7 Above: Tree species richness (species ha^{-1}) in low-várzea forests (LV), high-várzea forests (HV), and terra firme (TF) forests in the eastern, central, and western Amazon basin; and species similarity (circles) between LV and HV of the three regions (for details, see Wittmann et al. 2006a). Below: Overall tree species similarity (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)

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

Generally, the conditions for sustainable and integrated forest management and conservation are more favorable in the várzea than in the terra firme, as the former consists of highly productive forest ecosystems, has plenty of commercial timber species, and timber harvesting is simple and its costs are low (Schöngart et al. 2007).

The rapid depletion of nutrient stocks in the soils following the removal of large 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 m^3 ha^{-1} $year^{-1}$, and those of young successional stages are even higher, 43.7–51.9 m^3 ha^{-1} $year^{-1}$ (Schöngart 2003).

There are two options for timber management in the várzea: (1) the management of timber species in native floodplain forests such as carried out in the MSDR, in which a polycyclic (selection) system is applied by the community forest management, and (2) reforestation of degraded floodplain areas with timber species in monocultures, mixed cultures, or agroforest systems. The community forest management approach operates with a 25-year felling cycle, allowing the extraction of 4.57–5 trees ha^{-1}, corresponding to 0.55–2.37 m^3 ha^{-1} $year^{-1}$ (Schöngart and Queiroz 2010). The annual gross income is between US$ 15.42 and US$ 57.07 ha^{-1}. In terms of the productivity of várzea floodplain forests, these annual amounts of extracted volume or wood biomass can be annually renewed; nevertheless, there are concerns regarding the sustainability of this type of timber management (Schöngart 2008). Reforestation with fast-growing low-density tree species may locally reduce exploitation pressure on undisturbed forests, maintaining their ecological functions including climate control, biodiversity conservation, and watershed protection. Reforestation of deforested and degraded areas is likely to provide Brazil with credits from international carbon markets, within the framework of the Kyoto Protocol and decisions in the follow-up meetings of the United Nation Framework Convention of Climate Change (UNFCCC). The former specifically considers the emissions from sources and the removal by sinks that result from direct human-induced land-use change as well as forest-related activities (deforestation, reforestation, and afforestation) undertaken since 1990 (Binkley et al. 2002; Silver et al. 2004). Reforestation acts as a carbon sink since it results in the build-up of carbon stocks in the newly established biomass. When commercial harvests are accompanied by reforestation, the effect of C-losses by land-clearing is offset, over the long term, by C-sequestration and the accumulation of carbon stocks in the regenerating forest and by C-storage in long-lived wood and paper products. The GOL concept for sustainable timber production in the várzea and the reforestation of degraded and deforested areas together constitute a powerful instrument allowing community-based management to generate carbon credits in the future.

Fast-growing low-density tree species such as *F. insipida* (Schöngart et al. 2007) are of particular interest in terms of their potential for the reforestation of degraded areas. The lack of data on reforestation in Amazonian floodplains makes it difficult to estimate an economic value of timber production in plantation forests. Table 23.3 provides rough estimates for four commercial tree species of the várzea floodplain, two low-density tree species (*F. insipida* and *M. acaciifolium*) and two high-density tree species (*O. cymbarum* and *C. odorata*). Based on the relationships between diameter and crown area (Schöngart 2003), species-specific tree density ha^{-1} was estimated considering the MLD of a species (Rosa 2008; Schöngart 2008).

Table 23.3 Estimation of gross income and carbon sequestration for plantation forests in the várzea, referencing two low-density (*Ficus insipida, Macrolobium acaciifolium*) 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 ABWB (Mg C ha^{-1})[h]	MeanC-sequestration rate (Mg C ha^{-1} year^{-1})[i]
F. insipida	55	17	110	26.1	196	20.55	4,024	236.73	59.2	3.5
M. acaciifolium	49	54	131	24.7	178	23.89	4,251	78.72	72.5	1.3
C. odorata	38	45	196	21.7	144	66.67	9,579	212.87	67.5	1.5
O. cymbarum	53	63	115	25.7	191	34.44	6,570	118.26	109.9	1.7

[a] Data for minimum logging diameter (MLD) from (Rosa 2008; Schöngart 2008)

[b] Data for rotation period (time to reach MLD) from (Rosa 2008; Schöngart 2008)

[c] Tree density estimated by the relationship between diameter and crown area (10,000 m^2/crown area) (Schöngart 2003)

[d] Stand's basal area calculated by the basal area of the MLD multiplied by the tree density

[e] Stem 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)

[f] Wood prices indicated by Schöngart and Queiroz (2010) calculated based on an exchange rate of 1 US$ = 1.80 RS$

[g] Annual gross income estimated by dividing the gross income per hectare by the number of years of the rotation period

[h] Estimated by the equation: $AGWB = 0.0509 \times \rho \times H \times DBH^2$, where AGWB 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 AGWB for fast-growing low-density tree species and 50% for slow-growing high-density tree species (Clark et al. 2001; Elias and Potvin 2003)

[i] Estimated C-sequestration in AGWB during the rotation period

Relationships between diameter and stem height as well as stem height and form factor (Schöngart 2003) were used to estimate stem volumes per hectare for the four species and the results were then multiplied by the current wood prices (Schöngart and Queiroz 2010) in order to roughly estimate the gross income per hectare and year. The estimated annual gross income was found to vary three-fold among tree species, between US$ 237 ha^{-1} (*F. insipida*) and US$ 79 ha^{-1} (*M. acaciifolium*); 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 management (Fisher et al. 1992; McGrath et al. 1994; IBAMA 1994, 1997; Ruffino 1996), and the multiple use concept (Junk 2000a), have been developed in Amazonia or with special reference to the conditions there. At a global scale, the central Amazon floodplain is the best-studied floodplain in the tropics, despite the fact that the density of its human population is relatively low and modern research, which was initiated about a century ago, accelerated only after World War II (Junk and Piedade 2004).

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

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

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

Analyses of the production capacity of the different management systems and their environmental impacts on the várzea indicate that fishery has the highest production and the lowest environmental costs. Furthermore, there are many people directly and indirectly involved in activities related to fishery. Therefore, the sustainable management of fishery resources should have highest priority, and the activities of other stakeholders should be restricted when the impact on fish stocks becomes negative. The sustainable management of floodplain forests is another "várzea-friendly" activity. As summarized by Junk et al. (2010b), Amazonian floodplain forests are very diverse and highly adapted forests, with high productive potential in the fertile várzea. However, these forests require specific management methods, many of which remain to be tested in practice.

Subsistence agriculture in combination with subsistence fishery provides living conditions for many people in the várzea, although the economic return is relatively small. Agriculture directed at fruits and vegetables has a high production potential and economic return, but technologies and marketing have to be improved. Agriculture is labor intensive and thus retains many people within the várzea who would otherwise migrate to the cities. Because of the production of perishable goods, agriculture should be concentrated in areas located near urban centers. Agriculture destroys the floodplain forest of the species-rich high várzea and destabilizes the várzea in general by reducing the established system of protection against river currents during floods. Nonetheless, the area that can be exploited by farmers is relatively small thus there is no need to limit smallholder agriculture.

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

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

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

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

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

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Abstract This synthesis chapter provides an overview of the 23 chapters of this book. With more than 1000 tree species, Amazonian floodplain forests are the most diverse forests of this kind. They occur in different forms and under different hydrological and chemical (water and soil) conditions. Forests in nutrient rich whitewater river floodplains (várzeas) are richer in species, more dynamic, and more productive than those of black- and clearwater rivers. The new species colonization concept explains the relationship between upland and várzea forests. A model of forest succession is provided that indicates the development of different seral stages under different hydrological and sedimentological conditions. Trees react to long-term flooding and water-logging of the soils with many anatomical, morphological, physiological and phonological adaptations, which result in specific life history traits. Seed production, seedling establishment, and sapling survival are of fundamental importance for the regeneration of these forests and their reactions to the frequent set-backs caused by erosion and sedimentation processes. Until now, the use of floodplain forests has been restricted to highly selective timber exploitation, which depletes the stocks of the respective tree species. A management model, based on growth-oriented logging (GOL) is provided here. In this model, the extraction of the logs depends on water levels, the maximums and minimums of which can be predicted using new model based on sea surface water temperatures in the Pacific and the Atlantic Oceans. Such predictions would facilitate the management of the natural resources of the varzea, including management using forestry. When the many riparian forests are included, floodplain forests cover about one third of the Amazonian rain forest area. However, this fact has not been considered in management aspects and climate models for Amazonia. Global climate changes certainly will affect the hydrological cycle in Amazonia. However, we consider the prediction by the Hadley Center of a near “savannization” of the Amazon forest to be without sufficient scientific basis and unhelpful, because it may even accelerate the deforestation of Amazonia. The maintenance of intact wetlands will be very important for the sponge function of the landscape, which acts to retain water and to buffer extremely dry and wet periods. In this context, the floodplain forest is of utmost importance as a refuge for many plant and animal species.

24.1 Introduction

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 2010). 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 1984a; 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.

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

24.2 Age and Evolution of Amazonian Floodplain Forests

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

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

During Quaternary times periodic oscillations in global climate led to alternating glacial and interglacial periods which resulted in changes in the water level of the oceans worldwide (Irion et al. 2010). These changes affected the lower course of the Amazon River by increasing the slope during marine low water periods (Irion et al. 2010). 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 vàrzeas 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 (Irion et al. 2010).

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 Irion et al. (2010) 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 (Irion et al. 2010). 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 one million square kilometers to narrow stripes of riparian wetlands along streams and low order rivers. The first number has now been confirmed by the analysis of remote sensing data (Melack and Hess 2010). Extended wetlands occur in the upper Madeira River, the Negro River, the Araguaia River, and along the Amazon River and its white-water tributaries Purús, Juruá and Japurá. According to these authors, about 80% of the flooded area is covered by flood tolerant forest and shrubland. Our studies show that most of the wetlands along low order rivers are covered by riparian forest. If Junk's estimate of 1 million square kilometers of riparian wetlands holds true, the total area of forest subjected to periodic water logging or long term flooding increases to about 1.8 million square kilometers, corresponding to one fourth of the Amazon basin and 35% of the central Amazonian rain forest area of about 4.6 million square kilometres. The remaining 200,000 square kilometres belong to riparian forests in the *cerrado* belts. This estimate changes dramatically the view on the Amazon rain forest, which has been described largely as non flooded, *terra firme* forest. Flooding or water logging of the soil has to be considered an environmental factor that affects about 30% of the forests in the Amazon basin, with far reaching consequences for the physiology of the trees and edaphic processes, which affect the entire biome including the atmosphere. This aspect has been neglected so far in ecological studies concerning the role of the Amazon rain forest in the global climate change debate, as well as the impact of regional climate change scenarios on Amazonian wetlands and their vegetation.

Amazonian wetlands occur in great heterogeneity. A classification system is still missing, but urgently needed (1) for a better comparability of the results of wetland studies, (2) for the elaboration of research projects to close major gaps in wetland research, and (3) for the establishment of a national wetland policy to sustainably manage and protect wetlands and their resources, including biodiversity. First attempts to elaborate such a classification are ongoing in the State of Amazonas (Junk and Piedade 2005) and the Pantanal (Nunes da Cunha and Junk, in press). These classification efforts base on hydrological, water- and soil-chemical, and botanical parameters, as did Prance (1979), who elaborated the first classification system for Amazonian wetland forests. We consider this approach very useful and have adopted it with minor modifications (Junk and Piedade 2010; Table 24.1).

As Wittmann et al. (2010) have shown, species composition in floodplain forests varies considerably according to the position on the flooding gradient but also along the river axes and between river basins. Therefore the major classification units in Table 24.1 will be subdivided in future in different subunits according to species composition, as soon as enough regional data are available.

Table 24.1 Key to the principle types of Amazonian forests subject to inundation, according to Prance (1979), modified

Periodically inundated forests	
Flooded by regular annual cycles of rivers	
White-water	1. Seasonal várzea
Black-water and clear-water	2. Seasonal igapó
Flooded by tidal movements	
Saltwater	3. Mangrove
Freshwater backup	4. Tidal várzea
Flooded by irregular rainfall (flash floods)	5. Riparian forests along low-order rivers[a]
Long-term inundated forests[a]	
White-water	6. Várzea swamp forest, várzea chavascal[a]
Black-water and clear-water	7. Igapó swamp forest, igapó chavascal[a]

[a] Our modifications

24.4 Evolution, Species Diversity and the Tree Species Colonization Concept

24.4.1 Tree Species Diversity

Despite consisting of partially highly adapted and many endemic tree species, Amazonian floodplain forests are the most-species rich floodplain forests worldwide (Wittmann et al. 2010). 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. 2010).

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. 2010). Together with the evidence that high-várzea forests are floristically more similar to the uplands than low-várzea forests Wittmann et al. (2010) 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

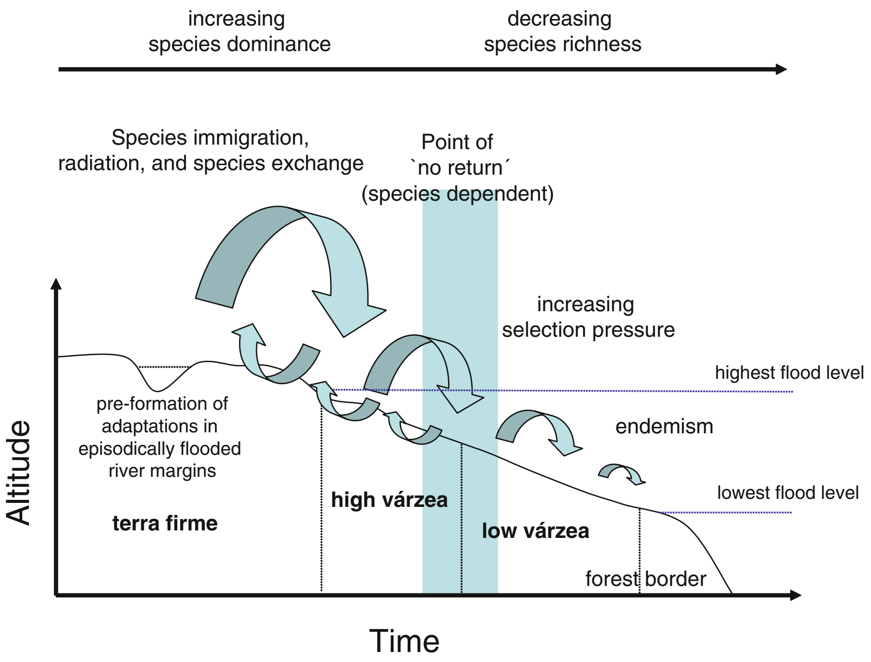

Fig. 24.1 Species Colonization Concept in várzea floodplains

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. 2010; Wittmann et al. 2010), 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. 2010). On the other hand, constantly migrating river-channels especially of the Amazonian white-water rivers affected large part of western equatorial Amazonia, and defined physical and chemical soil characteristics also within the substrates of recent uplands. Studying the flora of recent upland and floodplain forests thus provides data and evidences about landscape evolution, and allows for the creation of speciation and species distribution models in both the past and under future climate change. In this context, our knowledge about species migrations and the ecological interactions at the aquatic terrestrial transition zone (ATTZ; Junk et al. 1989) is extremely scarce. More comparative floristic inventories in both floodplain and terra firme forests are needed to fulfill this gap of knowledge in order to allow for reliable interpretations of the evolution of the Amazonian flora.

24.4.2 Floodplain Forests as Habitats for Associated Animal Species

The Amazonian floodplain forests provide important habitats for a large variety of animals. Best studied are the importance of the forests as food source for the fishes and the dispersal mechanisms of seeds (ichthyochory) (Parolin et al. 2010b; Goulding 1980). Large scale forest destruction will severely affect local fishery, because many commercially important fish species rely on fruit and seeds from the forest. Two monkey species, the White Uakari (*Cacajao calvus calvus*) and *Saimiri 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. Some of them are restricted to forest patches, many using scrub communities on lake sides and sand bars. Many wading birds use trees for resting at night and nesting. Petermann attributes the low number of forest bird species at Marchantaria island to the patchy distribution of forested areas, strong human disturbance and isolation of the island in the middle of the main channel of the Amazon River. This points to the importance of large, undisturbed forest areas for bird species diversity in Amazonian floodplains (Queiroz and Peralta 2010).

Of specific importance is the floodplain forest for species diversity of terrestrial invertebrates. Adis (1997) differentiates between terricolous and arboriculous species. Arboriculous species live mostly on the tree trunks or in the canopy. But many terricolous species also use the trees to escape flooding during the high water period. Periodic flooding reduces invertebrate species numbers in Amazonian floodplains in comparison to non-flooded habitats, but creates many specific survival strategies and endemic species.

An analysis of beetle communities in the canopies of different forest types confirms lower species diversity in the floodplains in comparison to terra firme forests but high site specific variability between different floodplain forest types. The authors relate these findings to greater tree species diversity in the terra firme, differences in tree species composition in the floodplain forests, and flood stress (Adis et al. 2010). The authors postulate that local deforestation will result in the loss of many unique restricted beetle species. This statement holds certainly true for terrestrial invertebrates in general.

24.5 Community Structure and Succession

Species distribution, diversity, and forest succession in Amazonian várzea forests is partially well-described. Abiotic variables, such as flood height and duration, sedimentation rates, distance from the main-river channels, soil texture, and solar radiation on the forest floor, but also biotic variables, including species richness, stand density, stand architecture, mean wood density, and increment and growth rates of trees, are variables that change during forest succession and interact with each other. Therefore, many várzea tree species can easily be classified as pioneer, secondary, or late-successional species, and the rules of forest succession allow for a certain predictability of forest type establishment and species diversity (Wittmann et al. 2010; Fig. 24.2).

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

There is, on the other hand, a gap of knowledge about species composition and diversity, forest structure, and succession in Amazonian igapó. The existing data 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. 2010). Due to the generally low sediment load of Amazonian blackwater rivers, igapó forests are characterized by the long-term stability of periodically flooded habitats. Combined with the paucity of nutrients, forest succession in Amazonian igapó occurs in longer time-scales than in Amazonian várzea, and trees are characterized by reduced growth rates (Schöngart et al. 2010), which possibly induce higher maximum tree ages than those reported for várzea trees (Schöngart et al. 2005). This directly influences the community structure of Amazonian igapó forests, and is an important trait for the management of forest resources. There is an urgent need for floristic inventories and ecological studies in Amazonian igapó, in order to create the basic knowledge about species composition, diversity variations, and tree growth behaviour in dependence of the abiotic environment.

24.6 Adaptations to Periodic Flooding

24.6.1 Morphological, Physiological and Phenological Adaptations

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

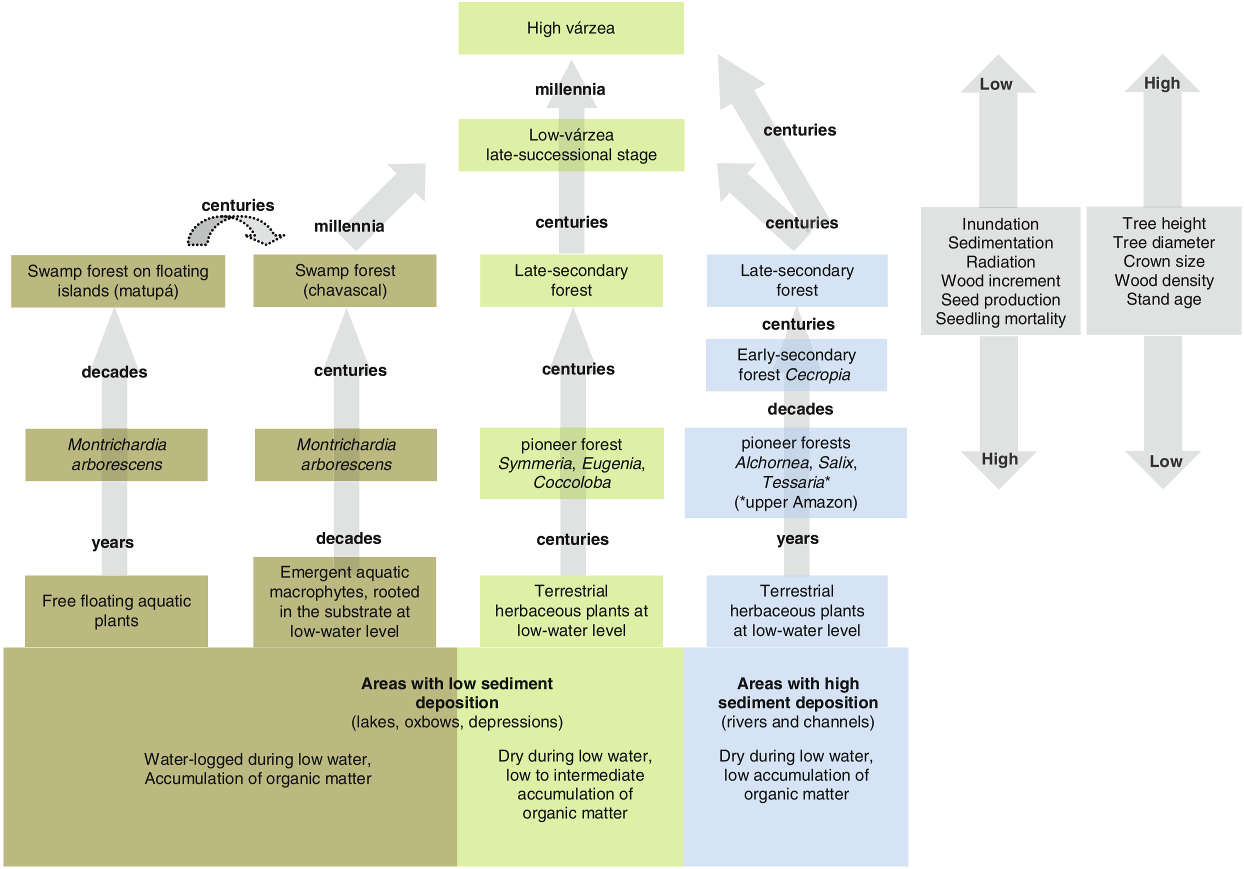

Fig. 24.2 Schematic model of forest succession in Amazonian várzea

Although in Amazonian floodplains the terrestrial phase is the main growth period for tree species, at high water the periods of limited growth last only few weeks, and new leaf flush, flowering, and fruiting occur in most trees while flooded (Parolin et al. 2010c). This requires a number of adaptations which allow growth despite waterlogging or submergence (Fig. 24.3).

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

In some species, the severe physiological stress caused by anoxic conditions in the root zone is indicated by a reduction of the transpiring surfaces via leaf shedding. In other species, the diurnal patterns of crown sap flow (a surrogate for transpiration) are influenced by the size of the stem water store that acts as internal water reservoir during the day and is refilled during the night. Individuals having larger internal water storage capacity, e.g. *Pseudobombax munguba* maintain maximum or near maximum transpiration rates for a longer period of time (Horna et al. 2010). Water limitation does not lead directly to drought damage on leaves but may indirectly

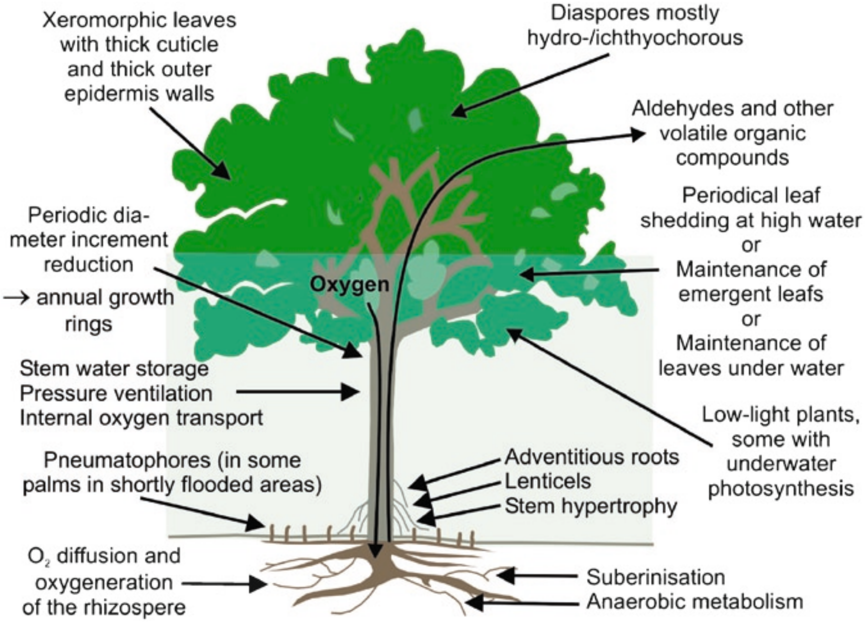

Fig. 24.3 Schematic presentation of morphologic, physiologic and phenologic adaptations of central Amazonian trees to periodic flooding

trigger leaf-shedding e.g. by hormone signals. Reduction in diameter increment of the stem during the flood period (ring formation, Worbes and Fichtler 2010) points to the flood stress for tree growth.

Since trees which have an active sap flow have a need for adequate supplies of carbohydrate also in the flooded period, a set of metabolic adaptations are required for survival and growth despite flooding (Horna et al. 2010). Among these metabolic adaptations we find a large amount of starch for energy supply in the roots of *Eugenia inundata*, a decrease of respiration and a switch to anaerobic pathways as shown for *Astrocaryum jauari* and *Macrolobium acaciifolium*.

A primary morphological plant strategy in response to flooding is the development of air spaces in the roots and stems which allow diffusion of oxygen from the aerial portions of the plant into the roots (Jackson and Armstrong 1999). Thus the roots do not have to depend on getting oxygen from the soil. Yet, different trees evolved different strategies to cope with the periodical flooding. Soil inundation usually inhibits root formation and branching, and growth of existing roots and mycorrhizae (Kozlowski 1997). This is not the case in Amazonian floodplains, where tree roots grow below water and mycorrhizae are not affected (Meyer et al. 2010; Haase and Rätsch 2010).

The different permeability of root types, which is determined by their morpho-anatomy and degree of suberinization, results in three main strategies described by De Simone et al. (2002b, 2003) and Haase and Rätsch (2010).

1 No suberinization and strong radial oxygen loss (ROL): Well oxygenated aerenchymatous adventitious roots which are able to build up a several millimeters thick oxygenated layer around the whole roots, suggesting a mechanism of detoxifying reduced phytotoxins by ROL. This is the case in the fast-growing pioneer *Salix martiana*.
2 Weak suberinization and limited ROL: Deposition of suberin in radial (Casparian bands) and tangential cell walls of the exodermis equips the root with a hydrophobic barrier that contributes to the plant's overall resistance. In this way, exchange between root and rhizosphere is not completely inhibited, enabling the loss of toxic ethanol, but also the entry of reduced phytotoxic compounds into the roots.
3 Strong suberinization and no ROL: A heavily suberized exodermis starting immediately behind the root tip limits radial oxygen loss (ROL) from the root to the rhizosphere in oxygen-depleted soils and inhibits the entry of toxic substances and infection by microbial pathogens but also inhibits release of ethanol, e.g. in *Tabernaemontana juruana*.

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

In contrast to the manifold adaptations at the root level, astonishingly the morpho-anatomy of leaves (Waldhoff and Parolin 2010) does not show a close relationship between leaf parameters and the periodicity of flooding. The measured variations, e.g. in leaf mass and size, are not understood as adaptations but rather as genetically fixed characteristics of the tree genera which immigrated from the terra firme. For example, the xeromorphic leaf structure found in the floodplain species (Waldhoff and Parolin 2010) is typical for trees of tropical forests in general. Xeromorphy helps to cope with insufficient water supply to the tree crowns during the aquatic phase, and with periods of drought occurring occasionally in the terrestrial phase. Apparently, the leaves which are not shed and maintain their functions despite prolonged submergence do not require different or additional morphological traits. The development of densely packed stacks in the chloroplasts and the low chlorophyll a/b ratio point to high photosynthetic efficiency under low light conditions, enabling the plants to maintain photosynthesis at low levels under water (Waldhoff and Parolin 2010). The same is true for leaf shedding which may not be a strategy against water loss but rather an endogeneously triggered rudiment related to the species' origin. Stem succulent trees of the Malvaceae family (former Bombacaceae) for example originate in semi-arid environments, drought avoidance being enhanced by leaf shedding. This behaviour may have facilitated immigration into the floodplains (Kubitzki 1989a, c), by overcoming first flood stress to water uptake by the fine root system.

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

24.6.2 Phylogenetic Development of Adaptations

Flooding stress is a strong driver of adaptive evolution (Jackson and Colmer 2005). The regularity of the recurrence of flooding, i.e. the predictability of the flood pulse (*sensu* Junk et al. 1989), enhances the evolution of specific adaptive traits and may have led to the large variety of species which are able to successfully colonize, establish and dominate the floodplains. Morphological adaptations may be remnants of pre-adaptations from the non-flooded terra firme species where floodplain trees originate from. The degree of flood tolerance may also depend on the time taken to colonize the floodplains. Some species have the potential for the development of adaptive traits – as revealed in waterlogging experiments with seedlings (Haase and Rätsch 2010) – but do not show them in the field in average years. For example, under natural conditions in the floodplains, adventitious roots, lenticels, or stem hypertrophy were observed only in few individuals probably due to the constant change in water level. Although not frequently encountered in the 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. 2010). 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 preselective 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. 2010).

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. Further research on the growth behaviour of floodplain tree species is needed to interpret different growth strategies as adaptation on flooding and/or other environmental factors.

A second explanation for the high energy reserves of seeds might be linked to the close relationship between seeds and fishes. Most Amazonian floodplain fruits eaten by fish have a high fat and protein content, so that the caloric value and delivered energy are high (Waldhoff et al. 1996; Parolin et al. 2010b). The costly allocation of energy reserves to the seeds makes sense in the light of long-distance dispersal, and even more when considering that fish can also transport seeds upriver against the water current. Long-distance dispersal plays an imminent role especially because the biota of Amazonian floodplains is less shaped by in situ speciation and radiation, but more by an equilibrium of immigration and extinction (Wittmann et al. 2010). This stands in contrast to most island and continental biotas and vegetational patterns, where the contrary is normal: the biota are mostly shaped by in situ speciation rather than an equilibrium of immigration and extinction (Price and Elliot-Fisk 2004).

As a first step to establishment, seed dispersal mechanisms play a crucial role, and are frequently linked to the abundant water in form of hydro- and ichthyochory (Parolin et al. 2010b). However, many animals involved in seed dispersal are also seed predators, and the efficiency of dispersal mechanisms has not been measured. Therefore the mere interpretation of the diaspore structure and the potential distribution mechanisms may result in misleading conclusions. Today, many of the tree species of the várzea forests are the most widely distributed in Amazonia, partially because of the persistence of floodplain forests along river systems during very long geological periods (Junk and Piedade 2010) and partly because of the ease of diaspore dispersal by water and fish.

Many floodplain tree species produce diaspores during the aquatic phases (Parolin et al. 2010c; Wittmann et al. 2010). The diaspores may float during variable periods on the water surface or sink to river and lake bottoms. The contact of the diaspores with the river water is controversially discussed in literature. While some authors interpret the contact with the water surface as to be the most important factor breaking seed dormancy, other authors argue that submergence prevents the seeds from oxygen supply that is necessary for respiration and to initiate germination (Oliveira Wittmann et al. 2010). In Amazonian várzea forests, viability of seeds that are in contact with the river water varies between 48 h (*Salix martiana*) to up to 5 months (*Piranhea trifoliata*). Germination experiments indicate that some várzea tree species show faster germination and higher germination rates when subjected to experimental flooding (Oliveira Wittmann et al. 2010). But our knowledge about the different germination strategies is extremely scarce and more germination experiments are necessary.

In contrast to the environmental conditions in Amazonian terra firme where seedling establishment is mainly keyed to the light-demand of tree species (i.e., Bazzaz and Pickett 1980; Denslow 1980; Whitmore 1989), seedling establishment in Amazonian floodplain forests is primarily determined by the flood pulse (Junk et al. 1989). Seedlings establish during the terrestrial phases and often must cope with full and prolonged submersion in the early life stages. Despite hypoxic conditions below water, in black- and whitewater they are deprived of light for many months due to low water transparency and suffer hypoxic or even anoxic conditions in soil and water. However, mortality rates in 459 seedlings of the várzea tree species *Eschweilera ovalifolia* and *Vitex cymosa* that were monitored before and after an aquatic phase in a low-várzea forests near Manaus (mean inundation depth 6.5 m, corresponding to 210 days year^{-1}) amounted to only 2.5% and 33%, respectively (Oliveira Wittmann et al. 2010), values that were surpassed by the establishment of new individuals of the same species during the following terrestrial phase.

Tree seedling establishment and mortality in várzea forests depend on forest succession, which is strongly interrelated to flooding (Wittmann et al. 2010). Most várzea tree species are well-adapted to very small ecological amplitudes and habitats, and forest succession implies that for most várzea species the optimal range of conditions are present only during a restricted period within the successional sere. Many of the trees do not successfully compete when regenerating at the same site as the parent trees. Despite the high impact of flooding, establishment of overall-dispersing early-successional species occurs frequently. Seedling densities in early-successional stages can amount to more than 2,000 individuals m^{-2} (Oliveira Wittmann et al. 2010). However, mortality rates in early-successional species amount to at least 99.98% (Wittmann et al. 2010). The proceeding forest succession and decreasing impact of flooding lead to an increased number of tree species with low but more efficient reproduction strategies. Seedling densities in late-successional forests are low, but so are mortality rates.

24.7 Photosynthesis, Primary Production, Biomass and Timber Production

24.7.1 Photosynthesis

Photosynthetic activities of Amazonian floodplain species change in the annual cycle, and the whole physiological apparatus is perfectly well adapted to the regular flood pulse. Under waterlogged conditions, most species show a reduction of mean CO_2-uptake in aerial leaves ranging from 10% (early successional *Cecropia latiloba*, *Senna reticulata*) to 20–50% (late successional *Nectandra amazonum*, *Crateva benthami*, *Tabebuia barbata*, *Vitex cymosa*) lower CO_2-uptake than in the terrestrial phase (Parolin et al. 2004b; Parolin et al. 2010a). CO_2-uptake rises again before the end of the flooded phase and remains high throughout the terrestrial phase (Parolin 2000a). Single measurements – in contrast to average values of the complete aquatic period – show that photosynthetic activity during waterlogging could reach the same or even higher values than in the terrestrial phase in almost all analysed species (Parolin 2000a). Waterlogged adults or seedlings of *Senna reticulata* often showed higher assimilation rates than non-flooded individuals: in a flooding experiment, waterlogged seedlings had an average assimilation rate which was 15 % higher than that of the well-watered control (Parolin 2001c). *Senna reticulata*, flooded by a water column of 4 m with only few leaves appearing above the water surface showed assimilation rates of up to 25 μmol CO_2 $m^{-2}s^{-1}$, which represent the highest photosynthetic activity measured in waterlogged Amazonian floodplain trees (Parolin 2001c). In several species, the influence of drought appeared to be by far more harmful than that of waterlogging or even submergence in terms of growth, photosynthetic performance and vitality after stress end (Waldhoff et al. 1998). In fact, drought may represent more of an impairment to survival than flooding to the local vegetation (Keel and Prance 1979; Scarano et al. 1994). This gains an increasing importance given the climatic changes which are predicted for the future in the Amazon basin (Malhi et al. 2008). Seedling recruitment and photosynthetic activity may become affected by increasing drought events and this may result in productivity changes and shifts of species composition.

24.7.2 Primary Production, Carbon Stock and Carbon Cycle

The high nutrient stocks in the alluvial soils (Furch 2000) and the periodic nutrient input by floods result in a high productivity of the várzea. A critical nutrient may be nitrogen, however the legume trees, which occur in large species and individual numbers, compensate possible nitrogen deficits by nitrogen fixation, which adds 17–20 kg N ha^{-1} $year^{-1}$ to the budget (Kern et al. 2010). Várzea forests are among the most productive tropical forest ecosystems worldwide with estimated aboveground net primary productions of 6.6–15.1 Mg C ha^{-1} $year^{-1}$ (Schöngart et al. 2010b). But carbon stocks and fluxes in aboveground coarse wood biomass (AGWB) differ considerably among floodplain forest types. Young successional stages have low carbon stocks in the AGWB, but high net carbon sequestration rates, while old-growth várzea forests have high C-stocks in the AGWB, but almost no net carbon sequestration. The carbon stock in the AGWB of the entire várzea forest ecosystem, however, is more or less balanced, since the carbon sequestrated during the first 50–100 years of primary succession is lost by natural tree mortality and forest destruction due to lateral erosion by the river and channel migration.

The carbon cycle in the AGWB of várzea forests differs considerably in comparison to the non-flooded terra firme forests. Central Amazonian várzea forests have C-storages in the AGWB with up to 120 Mg C ha^{-1}, while terra firme forests stocks about 116.0–195.5 Mg C ha^{-1} (Chambers et al. 2001). C-sequestration rates in the AGWB of várzea forests vary from 8.5 Mg C ha^{-1} $year^{-1}$ in the early successional stages to 2.7 Mg C ha^{-1} $year^{-1}$ in old-growth forests. In the terra firme old-growth forests the C-sequestration in the AGWB is about 2.1 Mg C ha^{-1} $year^{-1}$. This results in a two to three times lower mean carbon residence time in the várzea (higher C-turnover) when compared to non-flooded terra firme forests, characterizing the high dynamical processes of this ecosystem. But also the interannual short-term 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 rhythms of trees in both ecosystems with consequences in their function as short-term climate-induced carbon sinks and sources (Schöngart et al. 2002, this chapter b). The growth rhythms of trees in the terra firme are mainly controlled by the seasonal precipitation, while in the várzea forests these are mainly triggered by the flood-pulse.

The El Niño-Southern Oscillation originating from the equatorial Pacific associates both, the interannual variation in precipitation and flooding patterns in central Amazonia. It causes exceptional droughts during the rainy season in the Amazon leading to climate-induced C-releases from large regions of the terra firme to the atmosphere (Prentice and Lloyd 1998; Foley et al. 2002). During these events, however, parts of the várzea forests can be considered as C-sinks, because the flood-pulse is weakened and the extension of the vegetation period results in higher increment rates and thus higher C-sequestration rates (Schöngart et al. 2004). This duality of biogeochemical sinks and sources in adjacent forest ecosystems is not considered in existing estimates of carbon fluxes based on biogeochemical models, measurements of gas fluxes or accumulation of carbon in vegetation and soils in the Amazon basin. However, data on C-storage and C-sequestration available for floodplain forests still remain underrepresented considering their wide geographic distribution and different forest types as a result of varying climatic, edaphic and hydrologic factors. Especially for the igapó along black-water and clear-water rivers only very few estimates are available (Malhi et al. 2004; Stadtler 2007). These studies characterize the igapó forests as ecosystems with C-stocks in the AGWB in the range of várzea forests, but much lower C-sequestration rates and lower C-turnover. Tree-ring studies comparing tree growth of three species occurring in both systems under similar hydrological conditions confirmed the significant lower tree growth in the igapó compared to the várzea (Schöngart et al. 2005; Fonseca Júnior 2007).

Therefore igapó forest ecosystems, especially those along nutrient-poor black-water rivers, should be excluded from forest management activities and permanently protected by the creation of large conservation units (Schöngart 2010).

24.8 Actual Use and Management Options

24.8.1 Traditional and Modern Management Options of the Várzea

The várzea has been used and settled by a human population for centuries conducting agriculture, pasture, fishing, hunting, and the extraction of timber and non-timber products as a function of water-level fluctuations (Junk et al. 2010a). Commercial fishing occurs mainly during the low-water period, when fishes are concentrated in the remaining, often isolated water bodies.

Planting of crops is performed at the beginning of the terrestrial phase and the harvest at their end. Logging starts before the water reaches the forests and the timber is skidded and transported during the flooded period. In the Mamirauá Sustainable Development Reserve (MSDR), about 70% of the domestic income of an average household comes from fishery (Schöngart and Queiroz 2010) and consequently the income is high during the terrestrial phase and low during the high water period when economic activities are mainly restricted to timber extraction (Fig. 24.4).

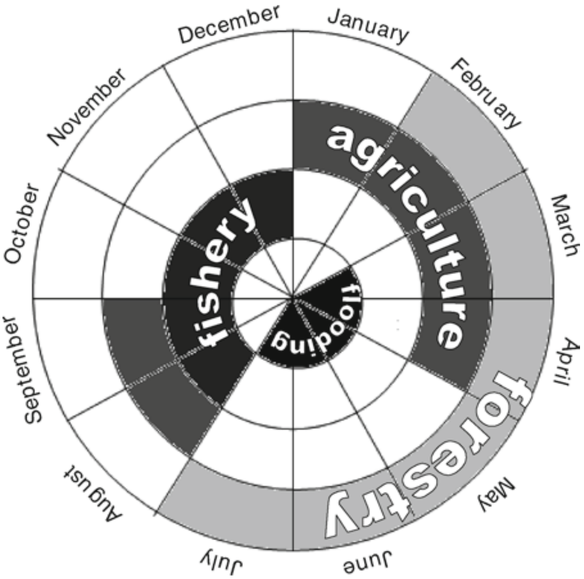

Fig. 24.4 Annual cycle of economic activities of riparian people in the Mamirauá Sustainable Development Reserve related to the seasonal variation of the water level

Management plans involving local communities have been successfully developed, tested and implemented in the MSDR based on a large number of environmental, biological-ecological and socio-economic studies (Queiroz and Peralta 2010). The community-based fishing of the giant pirarucu (*Arapaima gigas*), for instance, resulted in increasing fish populations and increasing incomes for the involved riverine population during the last ten years (Castello 2007).

Modern crop farming, animal ranching, fisheries and their impact on the várzea ecosystem have been studied near Manaus (Junk et al. 2000a). The following table indicates land and labor productivity of the different production systems (Junk et al. 2000b). Data on the land and labor productivity of the different production systems and calculations of timber productivity are presented in Junk et al. (2010a). An environmental impact analysis indicates cattle and water buffalo ranching as most detrimental for the environment because it destroys in large scale the floodplain forest for the establishment of natural and artificial pastures. Land productivity is low but compensated by relatively high labor productivity, resulting from a very low number of herdsmen employed by the ranchers. Negative impact is severe on fishery, habitat diversity and stability, and biodiversity. In contrast, the impact of selective logging is considered low when sustainability is guaranteed by adapted management methods, because it little affects fisheries and other environmental services (Junk et al. 2010a).

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. Highest water levels in Central Amazonia occur mostly in the 2nd half of June, while the lowest 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) 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 determent 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 phenom-

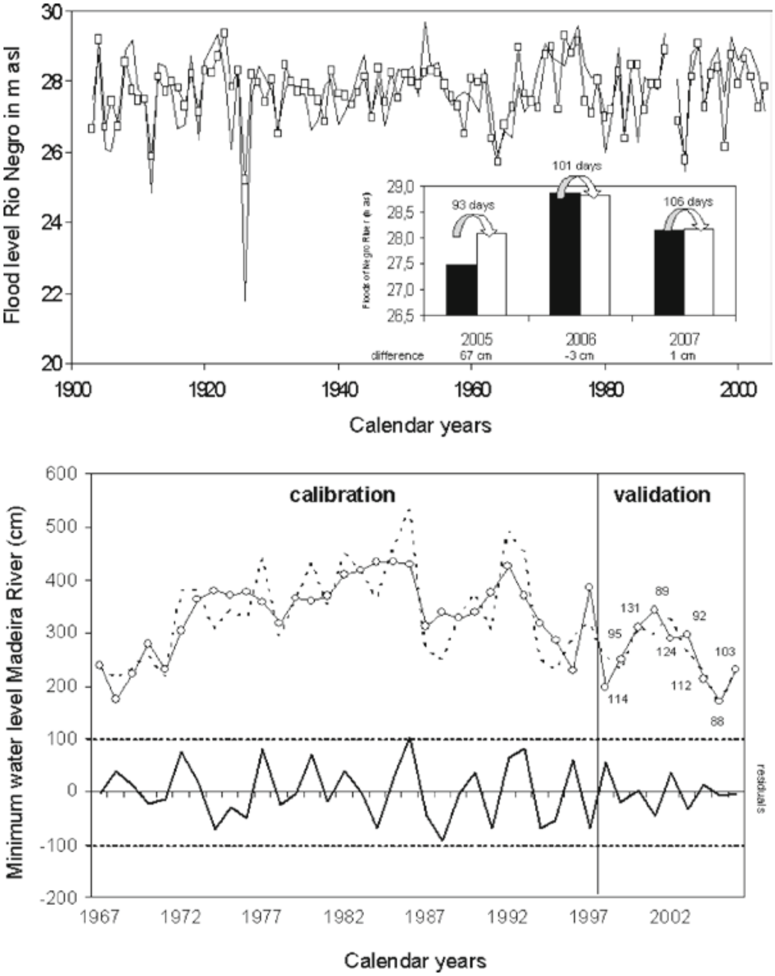

Fig. 24.5 Comparison between the observed (black line) and predicted (dotted line) maximum flood levels of the Negro River (Manaus) for the period 1903–2004 (Schöngart and Junk 2007). The forecasted maximum levels of the Negro River from 2005 to 2007, the difference between forecast (black bars) and 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)

enon 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 10–15% of the floodplain (Wittmann and Oliveira Wittmann 2010). Easy access 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) (Santos 1980). Although the area covered by floodplain forests is smaller than the accounted for by Amazonian 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 2010).

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 not 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 form 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 and Queiroz 2010).

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 and Queiroz 2010). 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 and Queiroz 2010). 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 Amazonian floodplains up to 87% of all tree species present in forest inventories are useful to the floodplain inhabitants, approximately 53% of all tree species provide NTFP in central Amazonian floodplains (Wittmann and Oliveira-Wittmann 2010). Many NTFP are of subsistence or indirect values to the inhabitants, and their value thus difficult to measure. Phytomedical products and edible fruits are among the most important use categories of NTFP in Amazonian floodplains, but a variety of other uses can be of huge local or even regional importance, such as fruits used as fish bait, fruits and wood for handicrafts, palm-heart extraction, latex and resins for fishing and hunting poisons, fibres for tying and braiding, oil, fuel, dyes, containers, or construction material in general (Wittmann and Oliveira-Wittmann 2010).

Ethnobotanical inventories about the uses of NTFP in floodplains are practically absent within the Brazilian part of the Amazon basin, and their economical importance including possible variations between the Amazonian flooded ecosystems and along the river system remains widely unknown. Most information about the use of forest resources originates from the Amerindian population, which may differ substantially from the use of colonialists. While the Net Present Value (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 NTFP. The value of many NTFP to the local inhabitants may be indirect and thus difficult to measure. Additionally, the NPV of phytomedical and phytocosmetical products is mostly unknown and/or undervalued by extractors, thus depriving inhabitants of a fair economic return. However, an increasing effort in ethnobotanical inventories could not only be important for the improvement of communally sustainable forest management plans, but it also would provide essential information for authorities about how to supply the rural population during periods with catastrophically low or high water levels.

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

The long–term success of forest management in the várzea and other multi-species forest ecosystems requires information on species-specific and site-specific growth rates to determine sustainable harvesting volumes and cutting cycles. However, the current Brazilian forest legislation considers only one cutting cycle and one minimum logging diameter (MLD) to manage a high variety of timber species of different forest types. In the várzea, there is the risk of overexploitation of slow-growing timber species, while the fast-growing timber species with low wood densities are not efficiently used (Schöngart 2010). The new concept "Growth-Oriented Logging – GOL" developed by Schöngart (2010), has been created as an aid to improve the forest management in the MSDR and central Amazonian várzea. GOL is based on species-specific and site-specific management criteria, such as 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 2010), such growth models and concepts can be established also for other timber species and forest types.

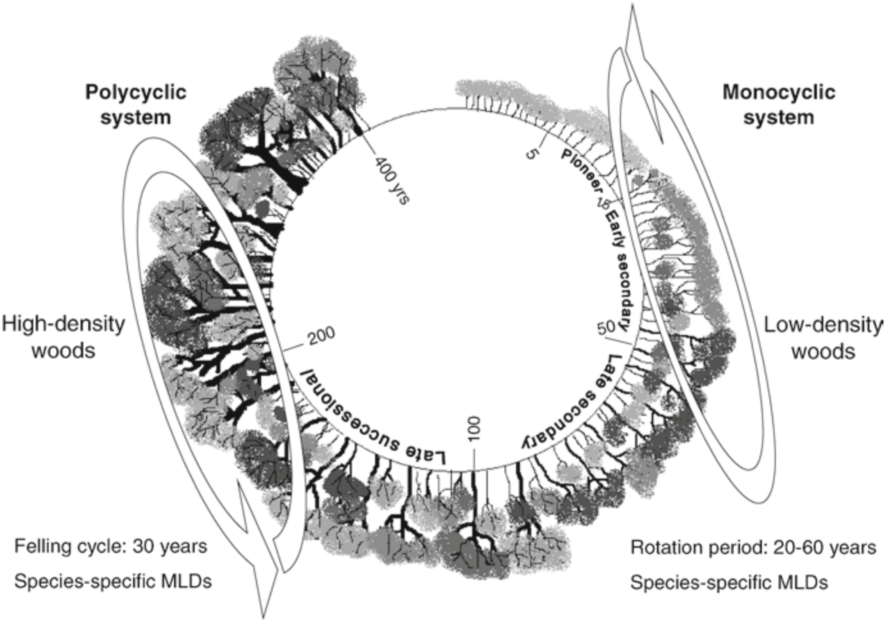

Fig. 24.6 GOL – Growth Oriented Logging: a silvicultural concept based on growth models derived from tree-ring analysis. The sustainable use of fast growing low-density woods in early and late secondary stages is achieved by monocyclic systems and that of slow growing high-density woods in late successional stages by polycyclic, selective systems (Schöngart 2010)

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. 2010). 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. 2010), these data serve for successful reforestation on degraded and deforested sites under optimal conditions, thus lowering the risks of failure.

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

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

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

Such experiences can be transferred to the floodplains of the Amazonian rivers where human populations depend on their natural resources to carry out agriculture, animal ranching, 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 dams nutrient-rich sediments will be retained in the artificial basins also favoring the accumulation of toxic materials like mercury due to the gold mining activities (Padovani et al. 1995). The increase of the water surface area in the artificial basins leads to extended water evaporation and the dams hinder the migration of many commercially important fish species which must reach the catchments for their reproductive cycle (Junk et al. 1997). These negative ecological and socio-economical impacts get more severe in the background of possible lower future water discharges in the large watershed caused by increasing SSTs in the tropical Northern Atlantic and tropical Pacific.

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

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

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

The predictions about precipitation changes are not yet clear, but a decrease of precipitation in the southern and northern Cerrado belts is probable. Precipitation amounts in the forested parts of Amazonia may continue at the same level but differences between dry and rainy season may increase, increasing the drought stress for the trees during the dry season. Global climate simulation models indicate increasing SSTs in the tropical ocean sectors for the forthcoming decades. This may cause more frequent lower maximum floods related to positive SST in the tropical Pacific (Schöngart and Junk 2007) and probably more frequent and severe droughts in the Amazonian floodplains associated with increased SSTs in the tropical North Atlantic. This points to water availability as the strongest stress factor in Amazonia.

Studies of Nepstad et al. (2001) show that already today, large parts of the terra firme rainforest in eastern Amazonia are vulnerable to fire during strong El Niño 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 (Sanford 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

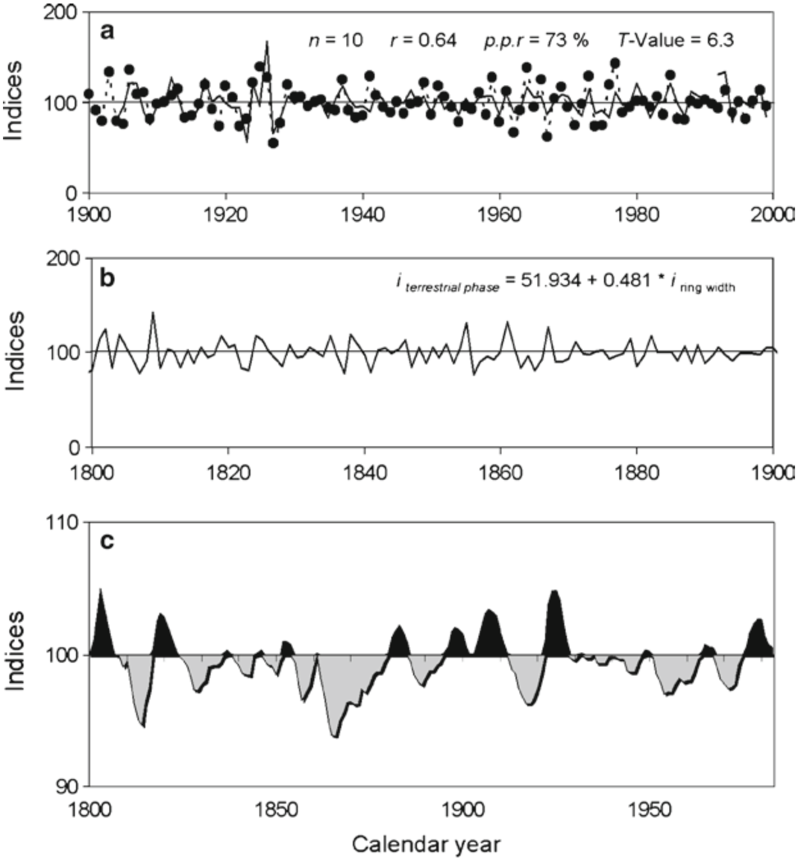

Fig. 24.7 Indexed ring-width chronology *Piranhea trifoliata* (dotted curve) and deseasonalized time series of the duration of the non-flooded period (black curve) derived from the daily recorded water-level at the port of Manaus. The correlation between the two curves is significant (*p.p.r* is the 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)

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 (Species Colonization Concept, Wittmann et al. 2010). Lateral and longitudinal genetic exchange plays an essential role in the development and maintenance of species diversity in the Amazon river floodplain. This holds true also for other species groups, such as fishes, birds, mammals and invertebrates, which live in the floodplain forests and depend on them. Additional genetic studies are required to clarify origin and relationship of the species and better explain speciation processes.

The fertile alluvial soils and the periodic flooding of white-water river floodplains provide the nutrient basis for high productivity despite intensive flood stress, which surpasses the productivity of central Amazonian upland forests by a factor 1.5 to 2 and that of the nutrient-poor igapó by a factor 2 to 2.5. Igapós grow on nutrient-poor soils and have no potential for sustainable timber production, but várzeas belong to the very few areas in central Amazonia, which can be used without risk of nutrient depletion. Growth Oriented Logging (GOL) (Schöngart 2010), provides the conceptional basis for sustainable forest culture with fast growing softwood species in areas covered by early successional stages and selected timber extraction of slow-growing hardwood species in advanced successional stages, without losing diversity, when substitution of the logged specimen is guaranteed by natural rejuvenation or plantation of saplings.

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

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

References

Aalto R, Maurice-Bourgoin L, Dunne T, Montgomery DR, Nittrouer CA, Guyot J-L (2003) Episodic sediment accumulation on Amazonian flood plains influenced by El Niño/Southern oscillation. Nature 425:493–497

Absy ML, Cleef A, Fournier M, Martin L, Servant M, Sifeddine A, da Silva F, Soubiès F, Suguio K, Turcq B, van der Hammen T (1991) Mise en évidence de quatre phases d'ouverture de la forêt dense dans le sud-est de L'Amazonie au cours des 60,000 dernières années. Première comparaison avec d'autres régions tropicales. Comptes Rendus Academie des Sciences Paris, Series II, 312, 673–678

Acuña C (1865) Novo descobrimento do grande rio das Amazonas. Rev Inst Hist e Geogr Bras 28(2):163–265

Adis J (1981) Comparative ecological studies of the terrestrial arthropod fauna in Central Amazonian inundation-forests. Amazoniana 7(2):87–173

Adis J (1997) Terrestrial invertebrates: survival strategies, group spectrum, dominance and activity patterns. In: Junk WJ (ed) The Central Amazon floodplain. Ecology of a pulsing system, pp 299–317. Ecolog Stud 126:535. Springer, Heidelberg

Adis J (2002) Amazonian Arachnida and Myriapoda – identification keys to all classes, orders, families, some genera, and lists of known terrestrial species. Pensoft Publishers, Sofia, p 590

Adis J, Latif M (1996) Amazonian arthropods respond to El Niño. Biotropica 28:403–408

Adis J, Furch K, Irmler U (1979) Litter production of a central Amazonian blackwater inundation forest. Tropical Ecology 20:236–245

Adis J, Erwin TL, Battirola LD, Ketelhut ZM (2010) The importance of floodplain forests for animal biodiversity: beetles in canopies of floodplain and upland forests. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Affonso AG, Novo EMLM, Melack JM, Hess LL (2007) Identificação e quantificação do desflorestamento nas áreas alagáveis nos municípios à margem do Rio Solimões/ Amazonas nos estados do Pará e Amazonas. Anais XIII Simpósio Brasileiro de Sensoriamento Remoto, Florianopolis, Brazil, pp 3235–3242

Agostinho AA, Gomes LC, Pelicice FM (2007) Ecologia e Manejo de Recursos Pesqueiros em Reservatórios do Brasil. Eduem, Maringá, Brazil, p 501

Aidar MPM, Martinez CA, Costa AC, Costa PMF, Dietrich SMC, Buckeridge MS (2002) Effect of atmospheric CO_2 enrichment on the establishment of seedlings of jatobá, *Hymenaea courbaril* L. (Leguminosae, Caesalpinioideae) Biota Neotropica 2(1). http://www.biotaneotropica.org.br/v2n1/en/abstract?article+BN01602012002

Aide TM (1993) Patterns of leaf development and herbivory in a tropical understory community. Ecology 74:455–466

Ainsworth EA, Davey PA, Bernacch CJ, Dermody OC, Heaton EA, Moore DJ, Morgan PB, Naidu SL, Yoora HS, Zhu XG, Curtins P, Long SP (2002) A meta-analysis of elevated [CO2] effects on soybean (*Glycine max*) physiology, growth and yield. Global Change Biology 8:695–709

Albernaz ALKM, Ayres JM (1996) Madeira para o uso sustentável e o monitoramento do recurso. Estação Ecológica Mamirauá: Bases científicas do plano de manejo, pp 73–130

Albernaz ALKM, Ayres JM (1999) Logging along the Middle Solimões River. In: Padoch C, Ayres JM, Pinedo-Vasquez M, Henderson A (eds) Várzea: diversity, development, and conservation of Amazonian's whitewater floodplains. The New York Botanical Garden Press, New York, pp 135–151

Alder D, Silva JNM (2000) An empirical cohort model for management of terra firme forests in the Brazilian Amazon. Forest Ecol Manag 130:141–157

Aleixo A (2006) Historical diversification of floodplain forest specialist species in the Amazon: a case study with two species of the avian genus *Xiphorhynchus* (Aves: Dendrocolaptidae). Biol J Linnean Soc 89:383–395

Alencar E (2002) Terra caída: encante, lugares e identidades. Ph.D. Thesis, Departamento de Antropologia, University of Brasília, Brazil

Alexander IJ (1989) Mycorrhizas in tropical forests. In: Proctor J (ed) Mineral nutrition in tropical forest and Savanna ecosystems. Blackwell Scientific, Oxford, pp 169–188

Alexander IJ, Höberg P (1986) Ectomycorrhizas of tropical angiospermous trees. New Phytol 102:541–549

Allaway WG, Curran M, Hollington LM, Ricketts MC, Skelton NJ (2001) Gas space and oxygen exchange in roots of *Avicennia marina* (Forssk.) Vierh. Var. *australasica* (Walp.) Moldenke ex N.C. Duke, the Grey Mangrove. Wetlands Ecol Manage 9:211–218

Allen ON, Allen EK (1981) The Leguminosae – a source book of characteristics, uses and nodulation. Macmillan, Basingstoke, London

Allen SE (1974) Chemical analysis of ecological material. Blackwell Scientific, Oxford

Almeida SS, Amaral DD, Silva ASL (2004) Análise florística e estrutura de florestas de Várzea no estuário amazônica. Acta Amazonica 34(4):513–524

Alonso-Zarazaga MA, Lyal HC (1999) A world catalogue of families and genera of Curculionoidea (Insecta: Coleoptera) (Exepting Scolytidae and Platypodiae). Entomopraxis, Barcelona, p 315. http://wtaxa.csic.es/

Alsdorf D, Dunne T, Melack JM, Smith L, Hess L (2005) Diffusion modeling of recessional flow on central Amazonian floodplains. Geophys Res Lett 32:L21405. doi:10.1029/2005GL024412

Alsdorf D, Bates P, Melack JM, Wilson M, Dunne T (2007) Spatial and temporal complexity of the Amazon flood measured from space. Geophys Res Lett 34:L08402. doi:10.1029/2007GL029447

Alves DS, Soares JV, Amaral S, Mello EMK, Almeida SAS, Silva OF, Silveira AM (1997) Biomass of primary and secondary vegetation in Rondônia, Western Brazilian Amazon. Global Change Biol 3:451–461

Alvim P de T, Alvim R (1978) Relation of climate to growth periodicity in tropical trees. In: Tomlinson PB, Zimmermann MH (eds) Tropical trees as living systems. Cambridge University Press, Cambridge, pp 445–464

Amaral P, Amaral Neto M (2005) Manejo florestal comunitário: processos e aprendizagens na Amazônia brasileira e na América Latina. IEB/IMAZON, Belém, Brazil

Amaral IL, Adis J, Prance GT (1997) On the vegetation of a seasonal mixedwater inundation forest near Manaus, Brazilian Amazonia. Amazoniana 14(3/4):335–347

Amarasekera KN, Lee RF, Williams ER, Eltahir EAB (1997) ENSO and the natural variability in the flow of tropical rivers. J Hydrol 200:24–39

Amstrong W (1978) Root aeration in the wetland condition. In: Hook DD, Crawford RMM (eds) Plant life in anaerobic environments. Ann Arbor Science, Michigan: 268–293

Andersen FO, Kristensen E (1988) Oxygen microgradients in the rhizosphere of the mangrove *Avicennia marina*. Mar Ecol Prog Ser 44:201–204

Andersen MC (1993) Diaspore morphology and seed dispersal in several wind-dispersed Asteraceae. Amer J Bot 80:487–492

Anderson AB, JrI M, Macedo DS (1999) Logging of *Virola surinamensis* in the Amazon floodplain: impacts and alternatives. In: Padoch C, Ayres JM, Pinedo-Vasquez M, Henderson A (eds) Várzea: diversity, development, and conservation of Amazonia's whitewater floodplains. The New York Botanical Garden Press, New York, pp 119–133

Anderson J, Saldana Rojas J, del Busto Rojas C (2005) Seed dispersal by a Neotropical fruit-eating fish. ESA Meeting Montreal. http://abstracts.co.allenpress.com/pweb/esa2005/document/?ID=49617

Anderson JM, Swift MJ (1983) Decomposition in tropical forests. In: Sutton SL, Whitemore TC, Chadwick AC (eds) Tropical rain forest: ecology and management. Blackwell Scientific, Oxford, pp 287–309

Andrade JL, Meinzer FC (1998) Regulation of water flux through trunks, branches, and leaves in trees of a lowland topical forest. Oecologia 115:463–471

Andreae MO, Rosenfeld D, Artaxo P, Costa AA, Frank GP, Longo KM, Silva-Dias MAF (2004) Smoking rain clouds over the Amazon. Science 303:1337–1340

Angeles G, Evert RF, Kozlowski TT (1986) Development of lenticels and adventitious roots in flooded *Ulmus americana* seedlings. Can J For Res 16:585–590

Angelov MN, Sung SS, Doong RL, Harms WR, Kormanik PP, Black CC (1996) Longand short-term flooding effects on survival and sink-source relationships of swamp-adapted tree species. Tree Physiol 16:477–484

Anhuf D, Motzer T, Rollenbeck R, Schröder B, Szarzynski J (1999) Water budget of the Surumoni-crane-site (Venezuela). Selbyana 20:179–185

Anhuf D, Ledru MP, Behling H, Da Cruz Jr FW, Cordeiro RC, Van der Hammen T, Karmann I, Marengo JA, de Oliveira PE, Pessenda L, Siffedine A, Albuquerque AL, da Silva Dias PL (2006) Paleo-environmental change in Amazonian and African rainforest during the LGM. Palaeogeograph Palaeoclimatol Palaeoecol 239:510–527

Antonik MM (2005) Population dynamics of *Mauritia flexuosa*: measuring the impact of white-lipped peccary on plant community structure in a tropical forest. Unpublished M.Sc. Thesis, State University New York, Syracuse, New York

APG II (The Angiosperm Phylogeny Group) (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Botan J Linn Soc 141:399–436

Appanah S (1985) General flowering in the climax rain forests of south-east Asia. J Trop Ecol 1:225–240

Araujo-Lima CARM, Goulding M, Forsberg M, Victoria R, Martinelli L (1998) The economic value of Amazonian flooded forest from a fisheries perspective. Verh Intern Verein Limnol 26:2177–2179

Armbrüster N (1999) Auswirkungen von Überflutung auf Photosynthese, Blattphysiologie und Phänologie zweier Baumarten des zentralamazonischen Überschwemmungswaldes. Diplomarbeit Uni Oldenburg, p 88

Armstrong J, Armstrong W (1988) *Phragmites australis* – A preliminary study of soil-oxidizing sites and internal gas transport pathways. New Phytol 108:373–382

Armstrong J, Jones RE, Armstrong W (2006) Rhizome phyllosphere oxygenation in *Phragmites* and other species in relation to redox potential, convective gas flow, submergence and aeration pathways. New Phytol 172:719–731

Armstrong W (1968) Oxygen diffusion from the roots of woody species. Physiol Plantarum 21:539–543

Armstrong W (1971) Radial oxygen losses from intact rice roots as affected by distance from the apex, respiration and waterlogging. Physiol Plant 25:192–197

Armstrong W (1979) Aeration in higher plants. Adv Bot Res 7:225–331

Armstrong W (1994) Polarographic oxygen electrodes and their use in plant aeration studies. Proc Royal Soc Edin 102B:511–527

Armstrong W, Drew MC (2002) Root growth and metabolism under oxygen deficiency. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half, 3rd edn. Marcel Dekker, New York, pp 729–761

Armstrong W, Brändle RA, Jackson MB (1994) Mechanism of flood tolerance in plants. Acta Botanica Neerlandica 43(4):307–358

Armstrong W, Cousins D, Armstrong J, Turner DW, Beckett PM (2000) Oxygen distribution in wetland plant roots and permeability barriers to gas-exchange with the rhizosphere: a micro-electrode and modeling study with *Phragmites australis*. Ann Bot 86:687–703

Ashford AE, Allaway WG (1995) There is a continuum of gas space in young plants of *Avicennia marina*. Hydrobiologia 295:5–11

Ashton PS, Givnish TJ, Appanah S (1988) Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. Am Naturalist 231:44–66

Asner GP (2001) Cloud cover in landsat observations of the Brazilian Amazon. Int J Remote Sens 22:3855–3862

Asner GP, Knapp DE, Broadbent EN, Oliveira PJC, Keller M, Silva JNM (2005) Selective logging in the Brazilian Amazon. Science 310:480–482

Assis RL (2008) Composição floristica e diversidade em clareiras de florestas sazonalmente alagáveis de várzea na Reserva de Desenvolvimento Sustentável Mamirauá, Amazônia Central. Master-Diss. Instituto Nacional de Pesquisas da Amazônia, Manaus

Augspurger CK (1981) Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinator and seed predators on *Hybanthus prunifolius* (Violaceae). Ecology 62:775–788

Augspurger CK, Franson SE (1993) Consequences for seed distributions of intra-crop variation in wing-loading of wind-dispersed species. In: Fleming TH, Estrada E (eds) Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer, Dordrecht, The Netherlands, pp 121–132

Ayres JM (1986) Uakaris and Amazonian flooded forest. Dissertation, Cambridge

Ayres JM (1993) As matas de várzea do Mamirauá. In: Sociedade civil Mamirauá (ed) Estudos de Mamirauá, vol.1. Sociedade civil Mamirauá, Mamirauá, pp 1–123

Ayres JM, Lima-Ayres DM, Albernaz A, Alves A, Moura E, Queiroz HL, Santos P, Barthem RB, Silveira R (1996) Mamirauá: um novo modelo de estação ecológica. Ciência Hoje 20(118):24–33

Ayres JM, Alves AR, Queiroz HL, Marmontel M, Moura E, Lima DM, Azevedo A, Reis M, Santos P, Silveira R, Masterson D (1998) Mamirauá. Die Erhaltung der Artenvielfalt in einem amazonischen Überschwemmungswald. In: Lourdes Davies de Freitas M (ed) Amazonien: Himmel der Neuen Welt, Bonn, pp 262–274

Ayres JM, Fonseca GAB, Rylands AB, Queiroz HL, Pinto LP, Masterson D, Cavalcanti RB (2005) Os corredores ecológicos das florestas tropicais do Brasil. Sociedade Civil Maminaurá, Belém, Brazil

Baas P (1990) Ecological trends in the wood anatomy and their biological significance. In: Schweingruber FH (ed) Anatomy of European woods. Eidg. Forschungsanstalt WSL, Paul Haupt, Bern, Stuttgart, pp 739–762

Babel U (1971) Gliederung und Beschreibung des Humusprofils in mitteleuropäischen Wäldern. Geoderma 5:297–324

Babel U (1979) Erfassung von Humusprofilmerkmalen mit Hilfe von Anschliffen. Zeitschr Pflanzenernährung Bodenkunde 142:195–205

Baillie IC (1989) Soil characteristics and classification in relation to the mineral nutrition of tropical wooded ecosystems. In: Proctor J (ed) Mineral nutrients in tropical forest and Savanna ecosystems. Blackwell Scientific, Oxford/London/Edinburgh, pp 15–26

Baker PA, Seltzer GO, Fritz SC, Dunbar RB, Grove MJ, Tapia PM, Cross SL, Rowe HD (2001) The history of South American tropical precipitation for the past 25, 000 years. Science 291:640–643

Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Monteagudo A, Neill DA, Núñez Vargas P, Pitman NCA, Silva JNM, Vásquez Martínez R (2004a) Increasing biomass in Amazonia forest plots. Philos T Roy Soc B 359:353–365

Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Killeen TJ, Laurance SG SG, Laurance WF, Lewis SL, Lloyd J, Monteagudo A, Neill DA, Patiño S, Pitman NCA, Silva JNM, Vásquez Martínez R (2004b) Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biol 10:545–562

Balick MJ (1985) Useful plants of Amazonia: a resource of global importance. In: Prance GT, Lovejoy TE (eds) Amazonia – key environments. Pergamon, New York, pp 339–368

Balslev H, Lutteyn J, Yllgaard B, Holm-Nielsen L (1987) Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. Opera Botanica 92:37–57

Bannerman M (2001) Mamirauá: a guide to the natural history of the Amazon flooded forest. Instituto de Desenvolvimento Sustentável Mamirauá – IDSM, Tefé, AM, Brazil

Barbosa C (2005) Sensoriamento Remoto da dinámica de circulação da água do sistema planície de Curai/rio Amazonas. Instituto Nacional de Pesquisas Espaciais, São José dos Campos, Brazil, p 281

Barthlott W (1990) Scanning electron microscopy of the epidermal surface in plants. In: Clauger D (ed): Application of the scanning EM in taxonomy and functional morphology. Systematics Association's Special Volume. Clarendon Press, Oxford, pp. 69–94

Barrios E, Herrera R (1994) Nitrogen cycling in a Venezuelan tropical seasonally flooded forest: soil nitrogen mineralization and nitrification. J Trop Ecol 10:399–416

Barros AC, Uhl C (1995) Logging along the Amazon river and estuary: patterns, problems, and potential. Forest Ecol Manage 77:87–105

Barros AC, Uhl C (1997) Padrões, problemas e potencial da extração madeireira ao longo do Rio Amazonas e do seu estuário. Imazon, Belém, Brazil, Série Amazônia N° 04

Barros AC, Uhl C (1999) The economic and social significance of logging operations on the floodplains of the Amazon estuary and prospects for ecological sustainability. In: Padoch C, Ayres JM, Pinedo-Vasquez M, Henderson A (eds) Várzea: diversity, development, and conservation of Amazonia's whitewater floodplains. The New York Botanical Garden Press, New York, pp 153–168

Barros FCM (2004) Avaliação da atividade imunológica In vitro de *Alchornea* spp. quanto à produção de peróxido de hidrogênio, óxido nítrico e fator de necrose tumoral-alfa por macrófagos murinos. M.Sc. – Diss. Faculdade de Ciências Farmacêuticas, Universidade Estadual Paulista, Araraquara

Barroso GM, Morim MP, Peixoto A, Ichaso CLF (1999) Frutos e Sementes: morfologia aplicada à sistemática de dicotiledôneas. Editora UFV, p 443

Barthem RB, Fabré NN (2004) Biologia e diversidade dos recursos pesqueiros da Amazônia. In: Ruffino ML (ed) A pesca e os recursos pesqueiros na Amazônia brasileira. IBAMA/ProVárzea, Manaus, pp 17–62

Batista VS, Inhamuns AJ, Freitas CEC, Freire-Brasil D (1998) Characterization of the fishery in river communities in the low-Solimões/high-Amazon region. Fish Manage Ecol 5:419–435

Bayley PB (1983) Central Amazon fish populations: biomass, production and some dynamic characteristcs. Ph.D. thesis, Dalhousie University. Halifax, Nova Scotia, Canada

Bayley PB (1998) Fisheries and aquatic biodiversity management in the Amazon. Desk Study. 98/055 CP-RLC to Food and Agriculture Organization, UN, Rome, Italy

Bayley PB, Petrere M Jr (1989) Amazon fisheries: assessment methods, current status, and management options. Canad Spec Publ Fish Aquat Sci 106:385–398

Bazzaz FA (1991) Regeneration of tropical forests: physiological responses of pioneer and secondary species. In: Gomez-Pompa A, Whitmore TC, Hadley M (eds) Rain forest regeneration and management. The Parthenon Publishing Group, London, pp 91–118

Bazzaz FA, Pickett STA (1980) Physiological ecology of tropical succession: a comparative review. Annu Rev Ecol System 11:287–310

Becker P (1996) Sap flow in Bornean heath and dipterocarp forest trees during wet and dry periods. Tree Physiol 16:295–299

Beerling DJ, Woodward FI (2001) Vegetation and the terrestrial carbon cycle: modeling the first 400 million years. University Press, Cambridge

Behling H, Keim G, Irion G, Junk W, Nunes De Mello J (2001) Holocene environmental changes in central Amazon basin inferred from Lago Calado (Brazil). Palaeogeograph Palaeoclimatol Palaeoecol 173:87–101

Benatti JH (2005) Aspectos jur´dicos e fundiários da várzea: uma proposta de regularização e gestão dos recursos naturais. In: Benfatti JH, Surgik ACS, Treccani GD, McGrath DG, da Gama ASP (eds) Aquestão fundiária e o maejo dos recursos naturais da várzea: análise para a elaboração de novos modelos jurídicos. ProVárzea/IBAMA, Manaus, Brasil, pp 77–100

Benecke U (1985) Tree respiration in steepland stands of *Nothofagus truncata* and *Pinus radiata*. Nelson, New Zealand. In: Turner T, Tranquillini W (eds) Establishment and tending of Subalpine forest: research and management. Eidg Anst Forstl Versuchswes 270, Berlin, pp 61–70

Bennett BC (2002) Forest products and traditional peoples: economic, biological, and cultural considerations. Nat Resour For 26:293–301

Bentes-Gama MM, Scolforo JRS, Gama JRV, De Oliveira AD (2002) Estrutura e valorização de uma floresta de várzea alta na Amazônia. Cerne 8(1):88–102

Benz RB, Rhode MJ, Cruzan BM (2007) Aerenchyma development and elevated alcohol dehydrogenase activity as alternative responses to hypoxic soils in the *Piriqueta caroliniana* complex. Am J Bot 94:542–550

Berg CC (1972) Olmediae, Brosimeae. Flora Neotrop 7:171

Berger WH, Wefer G (1992) Klimageschichte aus Tiefseesedimenten. Naturwissenschaften 79:541–550

Berish CW (1982) Root biomass and surface area in tree successional forests. Can J Forest Res 12:699–704

Bernoux M, Graça PMA, Cerri CC, Fearnside PM, Feigl BJ, Piccolo MC (2001) Carbon storage in biomass and soils. In: McClain ME, Victoria RL, Richey JE (eds) The biogeochemistry of the Amazon basin. Oxford University Press, London, pp 165–184

Beutler JA, Mc Call KL, Herbert K, Johnson T, Shoemaker RH, Boyd MR (2000) Cytotoxic clerodane diterpene esters from *Laetia corymbulosa*. Phytochemistry 55(3):233–236

Bewley JD, Black M (1982) Physiology and biochemistry of seed in relation to germination: viability, dormancy and environmental control. Springer, Berlin, p 375

Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I (2007) Cryptic species as a window on diversity and conservation. Trends Ecol Evolut 22:148–155

Binkley CS, Brand D, Harkin Z, Bull G, Ravindranath NH, Obersteiner M, Nilsson S, Yamagata Y, Krott M (2002) Carbon sink by the forest sector – options and needs for implementation. For Policy Econom 4:65–77

BIODAMAZ (2004) Diversidad de Vegetación de la Amazonía Peruana Expresada en un Mosaico de Imágenes de Satélite. Instituto de Investigaciones de la Amazonía Peruana (IIAP), Iquitos, Peru

Bischoff W-A, Siemens J, Kaupenjohann M (1999) Solute leaching into groundwater – A comparison of field methods considering preferential flow. Wasser Boden 51(12):37–42

Blair BC, Perfecto I (2001) Nutrient content and substrate effect on fine root density and size distribution in a Nicaraguan rain forest. Biotropica 33(4):697–701

Blokhina O, Virolainen E, Fagerstedt KV (2003) Antioxidants, oxidative damage and oxygen deprivation stress. Ann Bot 90:179–194

Blom CWPM (1990) Responses of flooding in weeds from river areas. In: Kawane S (ed) Biological approaches and evolutionary trends in plants. Academic Press, London, pp 81–94

Blom CWPM (1999) Adaptations to flooding stress: from plant community to molecule. Plant Biol 1:261–273

Blom CWPM, Voesenek LACJ (1996) Flooding: the survival strategies of plants. Tree 11(7):290–295

Bodmer RE (1990) Responses of ungulates to seasonal inundations in the Amazon floodplain. J Trop Ecol 6:191–201

Bolhár-Nordenkampf HR, Götzl M (1992) Chlorophyllfluoreszenz als Indikator der mit Seehöhe zunehmenden Streßbelastung von Fichtennadeln. FBVA Berichte Schriftenreihe d Forstl Bundesveranst 67:119–131

Bolhàr-Nordenkampf HR, Draxler G (1993) Functional leaf anatomy. In: Hall DO, Scurlock JJO, Bolhàr-Nordenkampf HR, Leegood RC, Long SP (eds) Photosynthesis and production in a changing environment. Chapman & Hall, London, pp 91–112

Bollmann A, Conrad R (1998) Influence of O_2 availability on NO and N_2O release by nitrification and denitrification in soils. Glob Change Biol 4:387–396

Boltz F, Carter DR, Holmes TP, Pereira R Jr (2001) Financial returns under uncertainty for conventional and reduced impact logging in permanent production forests of the Brazilian Amazon. Ecol Econ 39:387–398

Bongers F, Engelen D, Klinge H (1985) Phytomass structure of natural plant communities on spodosols in southern Venezuela: the Bana woodland. Vegetatio 63:13–24

Bongers F, Popma J, Del Castillo JM, Caraibas J (1988) Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. Vegetatio 74:55–80

Boot RGA, Gullison RE (1995) Approaches to developing sustainable extraction systems for tropical forest products. Ecol Appl 5:896–903

Borchert R (1991) Growth periodicity and dormancy. In: Raghavendra AS (ed) Physiology of trees. Wiley, New York, pp 21–245

Borchert R (1994a) Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology 75:1437–1449

Borchert R (1994b) Water status and development of tropical trees during seasonal drought. Trees 8:115–125

Borchert R, Rivera G (2001) Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. Tree Physiol 21:201–212

Bossel H, Krieger H (1991) Simulation model of natural tropical forests dynamics. Ecol Model 59:37–71

Bosshard HH (1984) Holzkunde, 2. Auflage, Bd. 2: Zur Bologie, Physik und Chemie des Holzes. Birkhäuser, Basel

Braca A, Morelli I, Mendez J, Battinelli L, Braghiroli L, Mazzanti G (2000) Antimicrobial triterpenoids from *Licania heteromorpha*. Planta Med 66(8):768–769

Brampton J (2001) Programa de Manejo Florestal Comunitário. Documento de trabalho. Instituto de Desenvolvimento Sustentável Mamirauá. MCT/CNPq-ProManejo-DFID, (unpublished)

Brandis D (1898) Forsteinrichtung in den Teakwaldungen von Pegu. Allg Forst Jagdztg 74:45–52

Brangham E (2000) História natural das várzeas de Mamirauá. Um guia de campo. SCM/IDSM, Belém, Brazil

Breen CM, Rogers KH, Ashton PJ (1988) Vegetation processes in swamps and flooded plains. In: Symoens JJ (ed) Vegetation of inland waters. Handbook of vegetation science. Kluwer, Dordrecht, pp 223–247

Brienen RJW, Zuidema PA (2005) Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. Oecologia 146:1–12

Brienen RJW, Zuidema PA (2006a) Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. J Ecol 94:481–493

Brienen RJW, Zuidema PA (2006b) The use of tree rings in tropical forest management: projecting timber yields of four Bolivian tree species. Forest Ecol Manag 226:256–267

Brienen RJW, Zuidema PA (2007) Incorporating persistent tree growth differences increases estimates of tropical timber yield. Front Ecol Environ 5:302–306

Brienza-Junior S, Yared YAG, Jarvis PG (1991) Agroforestry systems as an ecological approach in the Brazilian Amazon development. Agroforest Syst 45:319–323

Brondizio E, Moran E, Mausel P, Wu Y (1996) Land cover in the Amazon estuary – linking of the thematic mapper with botanical and historical data. Photogramm Eng Remote Sens 62:921–929

Broughton WJ, Jabbouri S, Perret X (2000) Keys to symbiotic harmony. J Bacteriol 182(20): 5641–5652

Brouwer LC (1996) Nutrient cycling in pristine and logged tropical rain forest – a study in Guyana. Tropenbos Guyana Series 1, Tropenbos Foundation, Utrecht

Brown S (1997) Estimating biomass and biomass change of tropical forests: a primer. FAO Forestry Paper 134, Rome, Italy

Brown S, Lugo AE (1992) Aboveground biomass estimates for tropical moist forests of Brazilian Amazon. Interciencia 17:8–18

Brown S, Gillespie A, Lugo A (1989) Biomass estimation methods for tropical forests with application to forest inventory data. Forest Sci 35:881–902

Bruce RW (2001) As florestas do Amazonas. Espécies, sítios, estoques e produtividade. Ministério do Meio Ambiente, Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (MMA/IBAMA), Brasilia, Brazil

Bruenig EF (1983) Vegetation structure and growth. In: Golley FB (ed) Tropical rain forest ecosystems. Structure and function. Elsevier, Amsterdam, pp 49–75

Bruenig EF (1996) Conservation and management of tropical rainforests. An integrated approach to sustainability. CAB International, Wallingford, UK

Bruenig EF (1998) Conservation and management of tropical rainforests: an integrated approach to sustainability, 2nd edn. CAB International, Wallingford, Oxfordshire

Bryant JA (1985) Fisiologia de semente. EPU, São Paulo, p 86

Buckeridge MS, Santos HP, Tiné MA, Aidar MPM (2004) Mobilização de reservas. In: Ferreira AG, Borguetti F (eds) Acúmulo de reservas. Germinação: do básico ao aplicado. Porto Alegre, Ed. Artmed, pp 163–185

Buckeridge MS, Mortari LC, Machado MR (2007) Respostas fisiológicas de plantas às mudanças climáticas: alterações no balanço de carbono nas plantas podem afetar o ecossistema? In: Rego GM, Negrelle RR, Morellato LPC (org.). Fenologia – Ferramenta pra a conservação e manejo de recursos vegetais arbóreos. Colombo, PR: Embrapa, pp 213–230

Buckley DP, O'malley DM, Apsit V, Prance GT, Bawa KS (1988) Genetics of Brazil nut (*Bertholletia excelsa* Humb. and Bonpl.): Lecythidaceae). I Genetic variation in natural populations. Theor Appl Genet 76:923–928

Budowski G (1961) Studies on forest succession in Costa Rica and Panama. Ph.D. thesis, New Haven, Yale University

Budowski G (1965) Distribution of tropical American rain forest species in the light of successional processes. Turrialba 15:40–42

Bueno CR, Yuyama K, Noda H, Filho DFS, Machado FM, de Paiva WO (2000) Non-conventional crops: a feasible alternative for Amazonian floodplains. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers bV, Leiden, pp 171–189

Bullock SH, Solís-Magallanes JA (1990) Phenology of canopy trees of a tropical deciduous forest in México. Biotropica 22:22–35

Burnham RJ, Graham A (1999) The history of neotropical vegetation: new developments and status. Ann Miss Bot Gard 86:546–589

Burnham RJ, Johnson KR (2004) South American palaeobotany and the origins of neotropical rainforests. Phil Trans R Soc Lond B 359:1595–1610

Burrows CJ (1990) Processes of vegetation change. Chapman & Hall, London

Buschmann C, Grumbach K (1985) Physiologie der Photosynthese. Springer, Berlin/Heidelberg/New York/Tokyo

Bush MB, Colinvaux PA, Wiemann MC, Piperno DR, Liu K (1990) Late Pleistocene temperature depression and vegetation change in Ecuadorian Amazonia. Quatern Res 34:330–345

Bush MB, Miller MC, De Oliveira PE, Colinvaux PA (2000) Two histories of environmental change and human disturbance in eastern lowland Amazonia. The Holocene 10:543–554

Cabral JA, McChesney JD, Milhouse WK (1993) A new antimalarial quassinoid from *Simaba guianensis*. J Nat Prod 56(11):1954–1961

Campbell DG, Daly DC, Prance GT, Maciel UN (1986) Quantitative ecological inventory of terra firme and várzea tropical forest on the Rio Xingu, Brazilian Amazon. Brittoniana 38:369–393

Campbell DG, Stone JL, Rosas A (1992) A comparison of the phytosociology and dynamics of three floodplain (Várzea) forests of known ages, Rio Juruá, western Brazilian Amazon. Bot J Linn Soc 108:213–237

Campbell IC, Poole C, Giesen W, Valbo-Jorgensen J (2006) Comparative biodiversity value of large wetlands: tonle Sap Great Lake, Cambodia. Aquat Sci 68:355–373

Camporese A, Balick MJ, Arvigo R, Espósito RG, Morsellino N, De Simone F, Tubaro A (2003) Screening of anti-bacterial activity of medicinal plants from Belize (Central America). J Ethnopharmacol 87(1):103–107

Cannell MGR (1984) Woody biomass of forest stands. Forest Ecol Manage 8:299–312

Cannon JG, Burton RA, Wood SG, Owen NL (2004) Naturally occurring fish poisons from plants. J Chem Educat 81(10):1457–1461

Cao K-F (2000) Leaf anatomy and chlorophyll content of 12 woody species in contrasting light conditions in a Bornean heath forest. Am J Bot 78:1245–1253

Carlquist S (1988) Comparative wood anatomy. Springer, Berlin/Heidelberg/New York

Carlquist S (2001) Comparative wood anatomy – systematic, ecological, and evolutionary aspects of dicotyledon wood, 2nd edn. In: Timell TE (ed) Springer series in wood science. Springer, Berlin, p 448

Carvalho JC (1998) Der Amazonas-Regenwald. In: Lourdes Davies de Freitas M (ed) Amazonien: Himmel der Neuen Welt. Bonn, pp 145–157

Carvalho JOP, Silva JNM, Lopes JCA (2004) Growth rate of a terra firme rain forest in brazilian Amazonia over an eight-year period in response to logging. Acta Amazonica 34(2):209–217

Castello L (2004) A method to count pirarucu (*Arapaima gigas)*: fishers, assessment, and management. N Am J Fish Mana 24(2):379–389

Castello L (2007) A socio-ecological synthesis on the conservation of the pirarucu (*Arapaima*) in floodplains of the Amazon. Ph.D. thesis, State University of New York, USA, p 212

Castro ABC (2004) Germinação e Crescimento de Plântulas de Espécies arbóreas da Várzea baixa da Amazônia Central. Trabalho de Conclusão de Curso para obtenção do Grau de Bacharel em Engenharia Florestal. Instituto de tecnologia da Amazônia – UTAM. Manaus, AM

Cattanio JH, Anderson AB, Carvalho MS (2002) Floristic composition and topographic variation in a tidal floodplain forest in the Amazon Estuary. Revista Brasileira de Botanica 25(4):419–430

Cattanio JH, Anderson AB, Rombold JS, Nepstad DC (2004) Phenology, litterfall, growth, and root biomass in a tidal floodplain forest in Amazon estuary. Revista Brasileira de Botânica 4:703–712

Cerdeira RGP, Ruffino ML, Isaac VJ (1997) Consumo de pescado e outros alimentos pela população ribeirinha do lago Grande de Monte Alegre. Acta Amazonica 27(3):213–227

Čermak J, Deml M, Penka M (1973) A new method of sap flow rate determination in trees. Biol Plant 15:171–178

Čermak J, Jenik J, Kucera J, Zidek V (1984) Xylem sap flow in a crack willow tree (*Salix frailis*) in relation to diurnal changes of the environment. Oecologia 64:145–151

Čermak J, Kucera J, Nadezhdina N (2004) Sap flow measurements with some thermodynamic methods, flow integration within trees and scaling up from sample trees to entire forest stands. Trees 18:529–546

Chabbi A, McKee KL, Mendelssohn IA (2000) Fate of oxygen losses from Typha domingensis (Typhaceae) and Cladium jamaicense (Cyperaceae) and consequences for root metabolism. Am J Bot 87:1081–1090

Chambers JQ, Higuchi N, Schimmel JP (1998) Ancient trees in Amazonia. Nature 391:135–136

Chambers JQ, Santos J, Ribeiro RJ, Higuchi N (2001) Tree damage, allometric relationships, and above-ground net primary production in Central Amazon forest. Forest Ecol Manag 152:73–84

Chao NL, Prang G (1997) Project Piaba – towards a sustainable ornamental fishery in the Amazon. Aquar Sci Conservat 1(2):105–111

Chapin FSIII, van Cleve K (1981) Plant nutrition adsorption and retention under differing fire regimes. In: Fire regimes and ecosystem properties. United States Forest Service Technical Report WO 26, pp 301–321

Chapman B, Siqueira P, Freeman A (2002) The JERS Amazon multi-season mapping study (JAMMS): observation strategies and data characteristics. Int J Remote Sens 23:1427–1446

Charriére M, Bourrel L, Gautier E, Pouilly M (2004) División geomorfológica del Río Mamoré. In: Pouilly M, Beck SG, Moraes M, Ibañez R, Ibañez C (eds) Diversidad biológica en la llanura de inundación del Río Mamoré. Importancia ecológica de la dinámica fluvial. Centro de Ecología Simón I. Patiño, Santa Cruz, Bolivia, pp 77–94

Chave J, Riéra B, Dubois M-A (2001) Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. J Trop Ecol 17:79–96

Chave J, Condit R, Aguilar S, Hernandez A, Lao S, Perez R (2004) Error propagation and scaling for tropical forest biomass estimates. Philos T Roy Soc B 359:409–420

Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Fölster H, Fromard F, Higuchi N, Kira T, Lescure J-P, Nelson BW, Ogawa H, Puig H, Riéra B, Yamakura T (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145:87–99

Clark DA (2002) Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. Ecol Appl 12:3–7

Clark DA (2004) Sources or sinks? The response of tropical forests to current and future climate and atmospheric compositions. Philos T Roy Soc B 359:477–491

Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J, Holland EA (2001) Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecol Appl 11:371–384

Clark DA, Clark DB (1994) Climate-induced annual variations in canopy tree growths in a Costa Rican tropical rain forests. J Ecol 82:865–872

Clark DA, Clark DB (1999) Assessing the growth of tropical rain forest trees: issues for forest modelling and management. Ecol Appl 9(3):981–997

Clark DA, Clark DB, Sandoval MR, Castro CMV (1995) Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. Ecology 76:2581–2594

Clark DA, Piper SC, Keeling CD, Clark DB (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. PNAS 100:5852–5857

Clark DB, Clark DA (1996) Abundance, growth and mortality of very large trees in neotropical lowland rain forest. Forest Ecol Manag 80:235–244

Clark DB, Clark DA, Read JM (1998) Edaphic variation and the mesoscale distribution of tree species in a neotropical rainforest. J Ecol 86:101–112

Clark JR, Benforado J (1981) Wetlands of bottomland hardwood forests. Developments in agricultural managed-forest ecology, vol. 11. Elsevier, Amsterdam/Oxford/New York

Clements FE (1936) Nature and structure of the climax. J Ecol 24:252–284

Cochrane MA (2003) Fire science for rainforests. Nature 421:913–919

Coe MT, Costa MH, Howard E (2007) Simulating the surface waters of the Amazon river basin: Impacts of new river geomorphic and dynamic flow parameterizations. Hydrol Processes 22: 2542–2553

Coe MT, Costa MH, Botta A, Birkett C (2002) Long-term simulations of discharge and floods in the Amazon Basin. J Geophys Res-Atmos 107(D20):8044. doi:10.1029/2001JD000740

Coe MT, Costa MH, Howard E (2009) Simulating the surface waters of the Amazon River basin: impacts of new river geomorphic and dynamic flow parameterizations. J Hydrol 369:165–174

Cole DW (1995) Soil nutrient supply in natural and managed forests. Plant Soil 168(169):43–53

Coley PD, Barone JA (1996) Herbivory and plant defenses in tropical forests. Ann Rev Ecol System 27:305–335

Colinvaux PA, de Oliveira PE, Bush MB (2000) Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypothesis. Quatern Sci Rev 19: 141–169

Colinvaux PA, De Oliveira PE (2001) Palaeoecology and climate of the Amazon basin during the last glacial cycle. J Quatern Sci 15:347–356

Colinvaux PA, Irion G, Räsänen ME, Bush MB, Nunes de Mello JAS (2001) A paradigm to be discarded: geological and paleoecological data falsify the Haffer and Prance refuge hypothesis of Amazonian speciation. Amazoniana 16:609–646

Colmenares OA, Teran L (1993) A biostratigraphic study of Paleogene sequences in southwestern Venezuela. Palynology 17:67–89

Colmer TD (2003) Long-distance transport of gases in plants: a perspective in internal aeration and radial oxygen loss from roots. Plant Cell Environ 26:17–36

Colmer TD, Cox MCH, Voesenek LACJ (2006) Root aeration in rice (*Oryza sativa*): evaluation of oxygen, carbon dioxide, and ethylene as possible regulators of root acclimatizations. New Phytol 170:767–778

Colmer TD, Gibberd MR, Wiengweera A, Tinh TK (1998) The barrier to radial oxygen loss from roots of rice (*Oryza sativa* L.) is induced by growth in stagnant solution. J Exp Bot 49(325):1431–1436

Colwell RK (2005) Estimates: statistical estimation of species richness and shared species from samples. http://viceroy.eeb.uconn.edu/estimates

Condit R (1995) Research in large, long-term tropical forest plots. Trends Ecol Evol 10:18–22

Condit R, Hubbell SP, Foster RB (1995) Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. Ecol Monogr 65:418–439

Condit R, Ashton PS, Baker P, Bunyavejchewin S, Gunatilleke S, Gunatilleke N, Hubbell SP, Foster RB, Itoh A, LaFrankie JV, Lee HS, Losos E, Manokaran N, Sukumar R, Yamakura T (2000) Spatial patterns in the distribution of tropical tree species. Science 288:1414–1418

Condit R, Pitman N, Leigh EG Jr, Chave J, Terborgh J, Foster RB, Percy Nunez V, Aguilar S, Valencia R, Villa G, Muller-Landau HC, Losos E, Hubbell SP (2002) Beta-diversity in tropical forest trees. Science 295:666–669

Connell EL, Colmer TD, Walker DI (1999) Radial oxygen loss from intact roots of Halophila ovalis as a function of distance behind the root tip and shoot illumination. Aqu Bot 63:219–228

Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and rain forest tress. In: den Boer PJ, Gradwell GR (eds.) Dynamics of populations. Proceedings of the advanced study institute on Dynamics of numbers in populations, Oosterbreek, 1970. Center for Agricultural Publishing and Documents, Wageningen, Netherlands, pp 298–312

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities in their role in community stability and organization. Am Nat 111:1119–1144

Conserva AS (2007) Germinação de sementes, emergência e recrutamento de plântulas de dez espécies arbóreas das várzeas da Reserva de Desenvolvimento Sustentável Amanã e Mamirauá, Amazônia Central. Tese – INPA/UFAM, Manaus, p 132

Cornell SE, Jickells TD, Cape JN, Rowland AP, Duce RA (2003) Organic nitrogen deposition on land and coastal environments: a review of methods and data. Atmos Environ 37:2173–2191

Costa M (2005) Estimate of net primary productivity of aquatic vegetation of the Amazon floodplain using Radarsat and JERS-1. Int J Remote Sens 26:4527–4536

Costa MH, Foley JA (2002) Combined effects of deforestation and doubled CO_2 concentrations on the climate of Amazonia. J Climate 13:18–34

Costa MH, Botta A, Cardille J (2003) Effects of large-scale change in land cover on the discharge of the Tocantins River, Amazonia. J Hydrol 283:206–217

Costa MPF, Novo EMLM, Ahern F, Mitsuo F, Mantovani JE, Ballester V, Pietsch RW (1998) The Amazon floodplain through radar eyes: Lago Grande de Monte Alegre case study. Can J Remote Sens 24:339–349

Coster C (1927) Zur Anatomie und Physiologie der Zuwachszonen und Jahresringbildung in den Tropen. Annales du Jardin botanique de Buitenzorg 37:49–160

Coster C (1928) Zur Anatomie und Physiologie der Zuwachszonen und Jahresringbildung in den Tropen. Annales du Jardin botanique de Buitenzorg 38:1–114

Cowell PJ, Roy PS, Jones RA (1992) Shoreface translation model: computer simulstion of coastal-sand-body response to sea-level rise. Math Comput Simulat 33:603–608

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408:184–187

Crawford RMM (1969) The physiological basis of flooding tolerance. Ber Dtsch Bot Ges 82(1/2):111–114

Crawford RMM (1978) Metabolic adaptations to anoxia. In: Hook DD, Crawford RMM (eds) Plant life in anaerobic environments. Ann Arbor Science, London, pp 119–136

Crawford RMM (1992) Oxygen availability as an ecological limit to plant distribution. Adv in Ecol Res 23:93–185

Crawford RMM (2003) Seasonal differences in plant responses to flooding and anoxia. Canad J Bot 81(12):1224–1246

Crawford RMM, Braendle R (1996) Oxygen deprivation stress in a changing environment. J Experiment Bot 47(295):145–159

Cromack K, Sollins P, Graunstein WC, Speidel K, Todd WA, Spycher G, Y-Li C, Todd RL (1979) Calcium oxalate accumulation and soil weathering in mats of the hypogeous fungus Hysterangium crassum. Soil Biol Biochem 11:463–468

Crook C, Clapp RA (1998) Is market-oriented forest conservation a contradiction in terms? Environ Conservat 25(2):131–145

Cullmann J, Junk JW, Weber G, Schmitz GH (2006) The impact of seepage influx on cation content of a Central Amazonian floodplain lake. J Hydrol 328:297–305

Curtis JT, McIntosh RP (1951) An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32(3):476–496

da Silvia GA, dos Santos BA, Alves MV, Maia LC (2001) Arbuscular mycorrhiza in species of Commelinidae (Liliopsida) in the State of Pernambuco (Brazil). Acta bot bras 15(2):155–165

Dacey JWH (1979) Methane efflux from lake sediments through water lilies. Science 203: 1253–1255

Dallmeier F, Kabel M, Foster RB (1996) Floristic composition, diversity, mortality and recruitment on different substrates: lowland tropical forest, Pakitza, Río Manu, Peru. In: Wilson DE, Sandoval A (eds) Manu – the Biodiversity of Southern Peru. Smithsonian Institute, Washington DC, pp 61–77

Darras S, Michou M, Sarrat C (1999) IGBP-DIS wetland data initiative – a first step towards identifying a global delineation of wetlands. IGBP Working Paper 19

Darwich A, Kern J, Robertson B, Souza E (2000) Decomposition of *Echinochloa polystachya* and its contribution to nutrient cycling in a Central Amazonian floodplain lake. Verh Internat Verein Limnol 27:2611–2614

Dauber E, Fredericksen TS, Peña M (2005) Sustainability of timber harvesting in Bolivian tropical forests. Forest Ecol Manag 214:294–304

Davis CC, Bel CD, Matthews S, Donoghue MJ (2002) Laurasian migration explains Gondwanan disjunctions: evidence from Malpighiaceae. Proc Natl Acad Sci 99:6833–6837

Davis CC, Fritsch PW, Bell C, Mathews S (2004) High latitude tertiary migrations of an exclusively tropical clade: evidence from Malphighiaceae. Int J Pl Sci 165:S107–S121

Dawkins HC, Philip MS (1998) Tropical moist forest silviculture and management: a history of success and failure. CAB International, Wallingford, UK

De Graaf NN, Filius AM, Huesca Santos AR (2003) Financial analysis of sustained forest management for timber: perspectives for application of the CELOS management system in Brazilian Amazonia. Forest Ecol Manag 177:287–299

De Jong W (2001) Tree and forest management in the flood plains of the Peruvian Amazon. Forest Ecol Manage 150:125–134

De Miranda AL, Silva JR, Rezende CM, Neves JS, Parrini SC, Pinheiro ML, Cordeiro MC, Pinto AC (2000) Anti-inflammatory and analgesic activity of the latex containing triterpenes from *Himatanthus sucuuba*. Planta Med 66(3):284–286

De Saizarbitoria CT, Anderson JE, Alfonso D, McLaughlin JL (1997) Bioactive furonaphtoquinones from *Tabebuia barbata* (Bignoniaceae). Acta Cient Venez 48(1):42–46

De Simone O (2003) Root adaptations of várzea tree species to prolonged flooding. Unpublished Ph.D. Thesis, University Oldenburg, p 125

De Simone O, Haase K, Müller E, Junk WJ, Gonsior GA, Schmitt W (2002a) Impact of root morphology on metabolism and oxygen distribution in roots and rhizosphere from two Central Amazon floodplain tree species. Funct Plant Biol 29:1025–1035

De Simone O, Müller E, Junk WJ, Schmid W (2002b) Adaptations of central Amazon tree species to prolonged flooding, Root morphology and leaf longevity. Plant Biol 4:515–522

De Simone O, Haase K, Müller E, Junk WJ, Hartmann K, Schreiber L, Schmidt W (2003a) Central amazon floodplain forests: root adaptations to prolonged flooding. Russ J Plant Physiol 50:848–855

De Simone O, Junk WJ, Schmidt W (2003b) Central Amazon floodplain forests: root adaptations to prolonged flooding. Russ J Plant Physiol 50(6):848–855

De Simone O, Junk WJ, Schmidt W (2003c) Apoplasmic barriers and oxygen transport properties of hypodermal cell walls in roots from four Amazonian tree species. Plant Physiol 132:206–217

De Souza ADL, Da Rocha AFI, Pinheiro MLB, Andrade CHS, Galotta AL, Dos Santos MPS (2001) Constituintes químicos de *Gustavia augusta* L. (Lecythidaceae). Química Nova 24(4):439–442

Denevan WM (1976) The aboriginal population of Amazonia. In: Denevan WM (ed) The native population of the Americas. University of Wisconsin Press, Madison, pp 205–234

Dennis ES, Dolferus R, Ellis M, Rahman M, Wu Y, Hoeren FU, Grover A, Ismond KP, Good AG, Peacock WJ (2000) Molecular strategies for improving waterlogging tolerance in plants. J Experiment Bot 51(342):89–97

Denslow JS (1980) Gap partitioning among tropical rain forest trees. Biotropica 12:47–55

Denslow JS (1987) Tropical rain forest gaps and tree species diversity. Ann Rev Ecol System 18:431–451

Dick CW, Abdul-Salim K, Bermingham E (2003) Molecular systematics reveals cryptic Tertiary diversification of a widespread tropical rainforest tree. Am Nat 160(12):691–703

Dick CW, Bermingham E, Lemes ML, Gribel R (2007) Extreme long-distance dispersal of the lowland tropical rainforest tree *Ceiba pentandra* L. (Malvaceae) in Africa and the Neotropics. Molec Ecol 16:3039–3049

Dick J, Skiba U, Munro R, Deans D (2006) Effect of N-fixing and non N-fixing trees and crops on NO and N_2O emissions from Senegalese soils. J Biogeogr 33:416–423

Dister E (1983) Zur Hochwassertoleranz von Auenwaldbäumen and lehmigen Standorten. Verhandlungen der Gesellschaft für Ökologie 10:325–336

Dittert K, Wötzel J, Sattelmacher B (2006) Responses of *Alnus glutinosa* to anaerobic conditions – mechanism and rate of oxygen flux into the roots. Plant Biol 8:212–223

Doignon-Bourcier F, Sy A, Willems A, Torck U, Dreyfus B, Gillis M, de Lajudie P (1999) Diversity of bradyrhizobia from 27 tropical Leguminosae species native of Senegal. System Appl Microbiol 22(4):647–661

Dong X, Zhang X (2000) Special stomatal distribution in *Sabina vulgaris* in relation to its survival in a desert environment. Trees 14:369–375

Downum K, Lee D, Hallé F, Quirke M, Towers N (2001) Plant secondary compounds in the canopy and understorey of a tropical rain forest in Gabon. J Trop Ecol 17:477–481

Doyle RD, Fisher TR (1994) Nitrogen fixation by periphyton and plankton on the Amazon floodplain at Lake Calado. Biogeochemistry 26:41–66

Drew MC, He C, Morgan PW (2000) Programmed cell death and aerenchyma formation in roots. Trends Plant Sci 3(5):123–127

Ducke A (1913) Explorações scientíficas no Estado do Pará. Bol Museu Paraense E Goeldi 7:100–198

Ducke A (1949) Arvores amazônicas e sua propagação. Bol Museu Paraense E Goeldi 10:81–92

Ducke A, Black GA (1953) Phytogeographical notes on the Brazilian Amazon. Anais Acad Brasil Ciênc 25:1–46

Ducke A, Black GA (1954) Notas sôbre a fitogeografia da Amazônia Brasileira. Bol Técn Inst Agron N 29:1–62

Duke JA, Vázquez R (1994) Amazonian Ethnobotanical dictionary. CRC Press, Florida, p p 215

Dünisch O, Bauch J, Sack M, Müller M (1999) Growth dynamics in wood formation of plantation-grown *Swietenia macrophylla* King and *Carapa guianensis* Aubl. Mitt Bundesforsch 193: 79–96

Dünisch O, Morais RR (2002) Regulation of xylem sap flow in an evergreen, a semi-deciduous, and a deciduous Meliaceae species from the Amazon. Trees 16:404–416

Dünisch O, Montóia VR, Bauch J (2003) Dendroecological investigations on *Swietenia macrophylla* King and *Cedrela odorata* L. (Meliaceae) in the central Amazon. Trees-Struct Funct 17(3):244–250

Dünisch O, Puls J (2003) Changes in content of reserve materials in an evergreen, a semi-deciduous, and a deciduous Meliaceae species from the Amazon. J Appl Bot 77:10–16

Dunne T, Mertes LAK, Meade RH, Richey JE, Forsberg BR (1998) Exchanges of sediment between the flood plain and channel of the Amazon River in Brazil. Geolog Socie Am Bull 110:450–467

Dunstan CA, Noreen Y, Serrano G, Cox PA, Perera P, Bohlin L (1997) Evaluation of some Samoan and Peruvian medicinal plants by prostaglandin biosynthesis and rat ear oedema assays. J Ethnopharmacol 57(1):35–56

Duque A, Sanchéz M, Cavelier J, Duivenvoorden JF (2002) Different floristic patterns of woody understorey and canopy plants in Colombian Amazonia. J Trop Ecol 18:499–525

Dutech C, Maggia L, Joly HI (2000) Chloroplast diversity in *Vouacapoua americana* (Caesalpinaceae), a neotropical forest tree. Molec Ecol 9:1427–1432

Dykstra JA, Heinrich R (1996) FAO model code of forest harvesting practice. Food and Agriculture Organization of the United Nations (FAO), Rome, Italy

Ebdon D (1998) Statistics in geography. Blackwell, Oxford

Edwards NT, Hanson PJ (1996) Stem respiration in a closed-canopy upland oak forest. Tree Physiol 16:433–439

Edwards NT, Shugart HH Jr, McLaughlin SB, Harris WF, Reichle DE (1980) Carbon metabolism in terrestrial ecosystems. In: Reichle DE (ed) Dynamic properties of forest ecosystems. Cambridge University Press, London, pp 499–536

Eiten G (1970) A vegetação do Estado de São Paulo. Bol Inst Botânica 7:1–147

Elias M, Potvin C (2003) Assessing intra- and inter-specific variation in trunk carbon concentration for 32 neotropical tree species. Can J Forest Res 33:1039–1045

Ellis MH, Dennis ES, James W (1999) Arabdopsis root and shoots have different mechanisms for hipoxic stress tolerance. Plant Physiol 119(1):57–64

El-Sohly HN, Joshi A, Li XC, Ross SA (1999) Flavonoids from *Maclura tinctoria*. Phytochemistry 52(1):141–145

Encarnación F (1993) El bosque y las formaciones vegetales en la llanura amazónica del Perú. Alma Máter 6:95–114

Engle DL, Melack JM (1993) Consequences of riverine flooding for seston and the periphyton of floating meadows in an Amazon floodplain lake. Limnol Oceanogr 38:1500–1520

Enstone DE, Peterson CA, Ma F (2003) Root endodermis and exodermis: structure, function, and responses to the environment. J Plant Growth Regul 21:335–351

Erwin TL (1983) Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. In: Sutton SL, Whitmore TC, Chadwick AC (eds) Tropical rainforest: ecology and management, pp 59–75. Blackwell Scientific, Oxford, p 498

Erwin TL (2005) Mapping patterns of β-diversity for beetles across the Western Amazon Basin: a preliminary case for improving inventory methods and conservation strategies. Proceedings of the California Academy of Sciences, series 4, 56 (Suppl. I)7:72–85

Eva HD, Miranda EE, Bella CM, Gond V, Huber O, Sgrenzaroli M, Jones S, Coutinho A, Dorado A, Guimaraes M, Elvidge C, Achard F, Belward AS, Batholomé E, Baraldi A, Grandi D, Vogt P, Fritz S, Hartley A (2002) A vegetation map of South America. European Commission, Joint Research Centre, EUR 20159 EN, p 34

Evans EE (2003) Aerenchyma formation. New Phytol 161:35–49

Fabian P, Kohlpaintner M, Rollenbeck R (2005) Biomass burning in the Amazon-fertilizer for the mountainous rain forest in Ecuador. Environ Sci Pollut Res 12:290–296

Fabré NN, Alonso JC (1998) Recursos ícticos no Alto Amazonas. Sua importância para as populações ribeirinhas. Boletim do Museu Paraense Emílio Goeldi, série Zoologia 14(1):19–55

Fahn A, Cutler DF (1992) Xerophytes. Gebrüder Borntraeger, Berlin

Fan L, Zheng S, Wang X (1997) Antisense suppression of phospholipase D retards abscisic acid- and ethylene-promoted senescence of postharvest Arabidopsis leaves. Plant Cell 9:2916–2919

Faria IF (2005) Ecoturismo: etnodesenvolvimento e inclusão social no Amazonas. PASOS 3(1):63–77

de Faria SM, Franco AA, de Jesus RM, de Menandro MS, Baitello JB, Mucci ESF, Döbereiner J, Sprent JI (1984) New nodulating legume trees from south-east Brazil. New Phytol 98:317–328

de Faria SM, Lewis GP, Sprent JI, Sutherland JM (1989) Occurrence of nodulation in the Leguminosae. New Phytol 111:607–619

de Faria SM, de Lima HC (1998) Additional studies of the nodulation status of legume species in Brazil. Plant Soil 200:185–192

de Faria SM, de Lima HC, Franco AA, Mucci ESF, Sprent JI (1987) Nodulation of legume trees from South East Brazil. Plant Soil 99:347–356

Farias ML (2007) Ecofisiologia de duas espécies arbóreas da várzea e da terra firme da Amazônia Central. Unpubl Master-Thesis, Universidade do Amazonas (UA), Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus

Farrell BD, Erwin TL (1988) Leaf-beetle community structure in an amazonian rainforest canopy. In: Jolivet P, Petitpierrre E, Hsiao TH (eds) Biology of chrysomelidae, pp 73–90. Kluwer, Dordrecht, p 615

Fearnside PM (1997) Wood density for estimating forest biomass in Brazilian Amazonia. Forest Ecol Manage 90:59–87

Fearnside PM, Guimarães WM (1996) Carbon uptake by secondary forests in Brazilian Amazonia. Forest Ecol Manag 80:35–46

Felsenstein J (1995) *PHYLIP (Phylogeny Inference Package),* Version 3.57c University of Washington

Fernandes-Corrêa AF, Furch B (1992) Investigations on the tolerance of several trees to submergence in blackwater (igapó) and whitewater (várzea) inundation forests near Manaus, Central Amazonia. Amazoniana 12:71–84

Ferreira LV (1997) Effects of the duration of flooding on species richness and floristic composition in three hectares in the Jaú National Park in floodplain forests in central Amazonia. Biodivers Conserv 6:1353–1363

Ferreira LV (1991) O efeito do periodo de inundação na zonação de comunidades, fenologia e regeneração em uma floresta de igapó na Amazonia Central. Master Thesis, INPA, Manaus, p 161

Ferreira CS (2002) Germinação e adaptações metabólicas e morfo-anatômicas em plântulas de *Himatanthus succuuba* (Spruce) Wood., de ambientes de várzea e terra firme na Amazônia Central. Unpubl Master Thesis, Universidade do Amazonas (UA), Instituto Nacional de Pesquisas da Amazônia (INPA), p 95

Ferreira CS (2006) Aspectos morfo-anatômicos, bioquímicos e genéticos de de *Himatanthus sucuuba*, em ambiente de várzea e de terra firme da Bacia Amazônica. Ph.D. thesis, CAPES, INPA/UFAM, Manaus

Ferreira CS, Piedade MTF, Parolin P, Barbosa KM (2005a) Tolerância da espécie *Himatanthus sucuuba* Wood. (Apocynaceae) ao alagamento na Amazônia Central. Acta Botanica Brasilica 19:425–429

Ferreira LV, Almeida SS, Amaral DD, Parolin P (2005b) Riqueza e composição de espécies da floresta de igapó e várzea da estação científica Ferreira Penna: Subsídios para o plano de manejo da Floresta Nacional Caxiuanã. Pesquisas Botânica 56:103–116

Ferreira CS, Piedade MTF, Bonates LC (2006) Germinação de sementes e sobrevivência de plântulas de Himatanthus sucuuba (Spruce) Wood. em resposta ao alagamento, nas várzeas da Amazônia Central. Acta Amazonica 36:413–418

Ferreira CS, Piedade MTF, Junk WJ, Parolin P (2007) Floodplain and upland populations of Amazonian Himatanthus sucuuba: effects of flooding on germination, seedling growth and mortality. Environ Experiment Bot 60(3):477–483

Ferreira CS, Piedade MTF, Franco A, Gonçalves JFC, Junk WJ (2008) Adaptive strategies to tolerate prolonged flooding in seedlings of floodplain and upland populations of Himatanthus sucuuba, a Central Amazon tree. Aquat Bot 1:1–7

Ferreira CS, Figueira AVO, Gribel R, Wittmann F, Piedade MTF (2010) Genetic variability, divergence and speciation in trees of periodically flooded forests of the Amazon: a case study of *Himatanthus sucuuba* (SPRUCE) WOODSON. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Ferreira LV (1998) Intraspecific variation in phenology in relation to flooding duration in *Eschweilera parviflora* (Lecythidaceae) in central Amazonian floodplain forest. An Acad Bras Ci 70:1–4

Ferreira LV (2000) Effect of flooding duration on species richness, floristic composition and forest structure in river margin habitats in Amazonian blackwater floodplain forests: implications for future design of protected areas. Biodivers Conserv 9:1–14

Ferreira LV, Prance GT (1998) Structure and species richness of low-diversity floodplain forest on the Rio Tapajós, Eastern Amazonia, Brazil. Biodivers Conserv 7:585–596

Ferreira LV, Almeida SS (2005) Relação entre altura de inundação, riqueza específica de plantas e o tamanho de clareiras naturais em uma floresta inundável de igapó na Amazônia central. Revista Árvore 29(3):445–453

Fichtler E, Clark DA, Worbes M (2003) Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and ^{14}C. Biotropica 35:306–317

Fichtler E, Trouet V, Beeckman H, Coppin P, Worbes M (2004) Climatic signals in tree rings of *Burkea africana* and *Pterocarpus angolensis* from semiarid forests in Namibia. Trees-Struct Funct 18:442–451

Fiedler S, Sommer M (2004) Water and redox conditions in wetland soils – their influence on pedogenic oxides and morphology. Soil Sci Soc Am 68:326–335

Field C, Mooney HA (1983) Leaf age and seasonal effects on light, water, and nitrogen use efficiency in a California shrub. Oecologia 56:348–355

Fine PVA, Mesones I, Coley PD (2004) Herbivores promote habitat specialization by trees in Amazonian forests. Science 305:663–665

Finegan B, Camacho M, Zamora N (1999) Diameter increment patterns among 106 tree species in a logged and silviculturally treated Costa Rican rain forest. Forest Ecol Manag 121:159–176

Fink S (1982) Histochemical investigations on starch-distribution and activity of acid-phosphatases in the xylem of some tropical tree species. Holzforschung 36:295–302

Fischer WR, Flessa H, Schaller G (1989) pH values and redox potential in microsites of the rhizosphere. Zeitschrift Pflanzenernährung Bodenkunde 152:191–195

Fisher AA, Corbet AS, Williams CB (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. J Anim Ecol 12:42–58

Fisher CFA, Chagas AL das GA, Dornelles LDC (1992) Pesca de águas interiores. IBAMA, Coleção Meio Ambiente. Série de Estudos de Pesca 2, Brasília, Brazil

Fittkau EJ (1982) Struktur, Funktion und Diversität zentralamazonischer Ökosysteme. Arch Hydrobiol 95(1/4):29–45

Fleming TH, Heithaus ER (1981) Frugivorous bat, seed shadows, and the structure of tropical forests. Biotropica 13:45–53

Foley JA, Botta A, Coe MT, Costa MH (2002) El Niño-Southern oscillation and the climate, ecosystems and rivers of Amazonia. Global Biogeochem Cy 16(4):1132. doi:10.1029/2002GB001872

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. Science 309:570–574

Fonseca Júnior SF (2007) Crescimento arbóreo de *Tabebuia barbata* (Bignoniaceae) e *Vatairea guianensis* (Fabaceae), em florestas alagáveis do igapó e várzea, na Amazônia Central, por métodos dendrocronológicos. M.Sc. thesis, INPA/UFAM, Manaus, Brazil

Fonseca Júnior SF, Piedade MTF, Schöngart J (2009) Wood growth of *Tabebuia barbata* (E. Mey.) Sandwith (Bignoniaceae) and *Vatairea guianensis* Aubl. (Fabaceae) in Central Amazonian black-water (igapó) and white-water (várzea) floodplain forests. Trees-Struct Funct 23(1):127–134

Forsberg BR, Hashimoto Y, Rosenqvist A, Miranda FP (2000) Tectonic fault control of wetland distributions in the Central Amazon revealed by JERS-1 radar imagery. Quaternary Int 72:61–66

Fortini LB, Rabelo FG, Zarin DJ (2006) Mixed potential for sustainable forest use in the tidal floodplain of the Amazon River. Forest Ecol Manag 231:78–85

Fosket DE (1994) Plant growth and development. A molecular approach. Academic Press. San Diego, CA, USA, p 580

Frailey CD, Rancy Lavina A, Souza Filho JP (1988) A proposed Pleistocene/Holocene lake in the Amazon basin and its significance to Amazonian geology and biogeography. Acta Amazonica 18(3–4):119–143

Frakes LA, Francis JE, Syktus JI (1992) Climate models of the Phanerozoic. Cambridge University Press, Cambridge

Franken M, Irmler U, Klinge H (1979) Litterfall in inundation, riverine and terra firme forests of Central Amazonia. Trop Ecol 20(2):225–235

Frankie GW, Baker HG, Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. J Ecol 62:881–899

Frankland B, Bartley MR, Spence DHN (1987) Germination under the water. In: Crawford RMM (ed) Plant life in aquatic and amphibious habitats, vol 5, Special publication series of the British ecological society. Blackwell Scientific, Oxford, England, pp 167–178

Frappart F, Seyler F, Martinez J-M, León JG, Cazenave A (2005) Floodplain water storage in the Negro River basin estimated from microwave remote sensing of inundation and water levels. Remote Sens Environ 99:387–399

Funck J (2004) Untersuchungen zur Wachstumsdynamik von *Cariniana micrantha* (Ducke) in der Nähe von Itacoatiara/Amazonien. M.Sc. Thesis, University Freiburg

Furch B (1984) Untersuchungen zur Überschwemmungstoleranz von Bäumen der Várzea und des Igapó. Blattpigmente. Biogeographica 19:77–83

Furch B, Fernandes-Corrêa AF, Mello JASN, Otto KR (1985) Lichtklimadaten in drei aquatischen Ökosysteme verschiedener physikalisch-chemischer Beschaffenheit. Amazoniana 9:411–430

Furch K (1997) Chemistry of várzea and igapó soils and nutrient inventory of their floodplain forests. In: Junk WJ (ed) The Central Amazon floodplain: ecology of a pulsing system. Ecolog Stud 126:47–68. Springer, Berlin/Heidelberg/New York

Furch K (1999) Zur Biogeochemie eines charakteristischen Überschwemmungsgebietes Zentralamazoniens, der Várzea auf der Ilha de Marchantaria nahe Manaus, Brasilien. Habilitationsschrift, University of Hamburg, p 454

Furch K (2000) Chemistry and bioelement inventory of contrasting Amazonian forest soils. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys, Leiden, pp 109–128

Furch K, Klinge H (1989) Chemical relationships between vegetation, soil and water in contrasting inundation areas of Amazonia. In: Proctor J (ed) Mineral nutrients in tropical forest and Savanna ecosystems. Blackwell Scientific, Oxford/London/Edinburgh, pp 189–204

Furch K, Junk WJ (1992) Nutrient dynamics of submersed decomposing Amazonian herbaceous plant species *Paspalum fasciculatum* and *Echinochloa polystachya*. Rev hydrobiol trop 25:75–85

Furch K, Junk WJ (1997a) Physicochemical conditions in floodplains. In: Junk WJ (ed) The Central Amazon floodplain: ecology of a pulsing system. Ecolog Stud 126:69–108. Springer, Berlin/Heidelberg/New York

Furch K, Junk WJ (1997b) The chemical composition, food value and decomposition of herbaceous plants and leaf-litter of the floodplain forest. In: Junk WJ (ed) The Central Amazon floodplain: ecology of a pulsing system. Ecolog Stud 126:187–206. Springer, Berlin/Heidelberg/New York

Gage JD, McAleece N (1979) Biodiversity professional. The National Museum of natural history, London. http://www.worldagroforestrycentre.org/sites/rsu/resources/biodiversity/software/biodiversityprofessional.asp

Gama JRV, Bentes-Gama MM, Scolforo JRS (2005a) Manejo sustentado para floresta de várzea na Amazônia Oriental. Revista Árvore 29(5):719–729

Gama JRV, De Souza AL, Martins SV, De Souza DR (2005b) Comparação entre florestas de várzea e de terra firme do estado do Pará. Revista Árvore 29(4):607–616

Garcia-Montiel DC, Melillo JM, Steudler PA, Tian H, Neill C, Kicklighter DW, Feigl B, Piccolo M, Cerri CC (2004) Emissions of N_2O and CO_2 from terra firme forests in Rondonia, Brazil. Ecol Appl 14:S214–S220

Gardner WK, Barber DA, Parbery DG (1983a) The acquisition of phosphorus by Lupinus albus L. III. The probable mechanism by which phosphorus movement in the soil/root interface is enhanced. Plant Soil 70:107–114

Gardner WK, Barber DA, Parbery DG (1983b) The acquisition of phosphorus by Lupinus albus L V. The diffusion of exudates away from roots: a computer simulation. Plant Soil 72:13–29

Gascon C, Malcolm JR, Patton JL, da Silva MNF, Bogard JP, Lougheed SC, Peres CA, Neckel S, Boag PT (2000) Riverine barriers and the geographic distribution of Amazonian species. Proceedings of the National Academy of Sciences, USA, vol 97, pp 13672–13677

Gaston S, Zabalza A, González EM, Arrese-Igor C, Aparicio-Tejo PM, Royuela M (2002) Imazethapyr, an inhibitor of the branched-chain amino acid biosynthesis, induces aerobic fermentation in pea plants. Physiol Plant 114:524–532

Gehring C, Vlek PLG (2004) Limitations of the ^{15}N natural abundance method for estimating biological nitrogen fixation in Amazonian forest legumes. Basic Appl Ecol 5:567–580

Gentil JML (1988) A juta na agricultura de várzea na área de Santarém – Méio Amazonaas. Bol Museu Paraense E Goeldi 4(2):118–199

Gentry AH (1974) Flowering phenology and diversity in tropical Bignoniaceae. Biotropica 6:64–68

Gentry AH (1986) Endemism in tropical versus temperate plant communities. In: Soulé ME (ed) Conservation biology. Sinauer, Sunderland

Gentry AH (1987) Tree species richness in upper Amazonian forests. Proceedings of the National Academy of Sciences, USA, vol 85, pp 156–159

Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. Ann Mo Botan Gard 75:1–34

Gentry AH (1992) Tropical forest biodiversity: distributional patterns and their conservational significance. Oikos 63:19–28

Gerwing JJ (2002) Degradation of forests through logging and fire in the eastern Brazilian Amazon. Forest Ecol Manag 157:131–141

Gessner F (1968) Zur ökologischen Problematik der Überschwemmungswälder des Amazonas. Int Rev Ges Hydrobiol 53(4):525–547

Gill CJ (1970) The flooding tolerance of woody species – a review. Forest Abstr 31(4):671–688

Givnish T, Vermeij G (1976) Sizes and shapes of liane leaves. Am Nat 110:743–778

Godoy JR, Petts G, Salo J (1999) Riparian flooded forests of the Orinoco and Amazon basin: a comparative review. Biodivers Conserv 8:551–586

Goeldi EA (1904) Against the destruction of white herons and red ibises on the lower Amazon, especially on the Island of Marajó. Pará, Brazil

Goldstein G, Andrade JL, Meinzer FC, Holbrook NM, Cavelier J, Jackson P, Celis A (1998) Stem water storage and diurnal patterns of water use in tropical forest canopy trees. Plant Cell Environ 1:397–406

Golley FB (1961) Energy values of ecological materials. AEC, Savannah River Project, University of Georgia. Ecology 42:581–584

Gonçalves AL, Alves Filho A, Menezes H (2005) Estudo comparativo da atividade antimicrobiana de extratos de algumas árvores nativas. Arq Inst Biol São Paulo 72(3):353–358

Good AG, Crosby WL (1989) Anaerobic Induction of Alanine Aminotransferase in Barley Root Tissue. Plant Physiol 90:1305–1309

Good JEG, Winder JD, Sellers E, Williams TG (1992) Species and clonal variation in growth responses to waterlogging and submersion in the genus *Salix*. Proc Royal Soc Edin 98B: 21–48

Gorchov DL, Cornejo F, Ascorra CF, Jaramillo M (1995) Dietary overlap between frugivorous birds and bats in the Peruvian Amazon. Oikos 74:235–250

Gottsberger G (1978) Seed dispersal by fish in inundated regions of Humaitá, (Amazonas). Biotropica 10:170–83

Gottsberger G, Silberbauer-Gottsberger I (2006) Life in the Cerrado. Vol II Pollination and seed dispersal. Reta, Ulm

Goulding M (1980) The fishes and the forest, exploration in Amazonian natural history. University of California Press, Berkeley/Los Angeles/London

Goulding M (1983) The role of fishes in seed dispersal and plant distribution in Amazonian floodplain ecosystems. Sonderbd Naturwiss Ver Hamburg 7:271–283

Goulding M, Carvalho ML, Ferreira EG (1988) Rio Negro, rich life in poor water. SPB Academic Publishing, The Netherlands

Goulding M, Smith NJH, Mahar DJ (1996) Floods of fortune: ecology and economy along the Amazon. Columbia University Press, New York, p 193

Gourou P (1950) Observações Geográficas na Amazônia. Revista Brasileira Geográfica no. 3:49–102

van den Graaf AA, Mulder A, de Bruijn P, Jetten MSM, Robertson LA, Kuenen JTG (1995) Anaerobic oxidation of annonium is a biologically mediated process. Appl Env Microb 61(4):1246–1251

Grace J, Lloyd J, McIntyre J, Miranda AC, Meir P, Miranda HS, Nobre CA, Moncrieff J, Massheder J, Malhi Y, Wright I, Gash J (1995) Carbon dioxide uptake by an undisturbed tropical rain forest in Southwest Amazonia. Science 270:778–780

Grace J, Malhi Y (2002) Carbon dioxide goes with the flow. Nature 416:594–595

Graffmann KC (2000) Die Bedeutung der Druckventilation für die Sauerstoffversorgung des Wurzelsystems bei Bäumen der amazonischen Überschwemmungswälder. Dissertation Uni Köln, p 91

Graffmann KC, Grosse W, Junk WJ, Parolin P (2008) Pressurized gas transport in Amazonian floodplain trees. Environ Experiment Bot 62:371–375

Granier A (1985) Une nouvelle methode pour la mesure du flux de seve brute dans le tronc des abres. Ann Sci For 42:193–200

Granier A (1987) Mesure du flux de seve brute dans le tronc du Douglas par une nouvelle methode thermique. Ann Sci For 42:193–200

Granier A (1996) Sap flow measurements using the radial flowmeter technique. INRA–Unité d'Ecophysiologie Forestière, Champenoux

Granier A, Bobay V, Gash JHC, Gelpe J, Saugier B, Shuttleworth WJ (1990) Vapour flux density and transpiration rate comparisons in a stand of Maritime pine (*Pinus pinaster* Ait.) in Les Landes forest. Agric For Meteorol 51:309–319

Granier A, Anfodillo T, Sabatti M, Cochard H, Dreyer E, Tomasi M, Valentini R, Breda N (1994) Axial and radial water flow in the trunks of oak trees: a quantitative and qualitative analysis. Tree Physiol 14:1383–1396

Granier A, Biron P, Breda N, Pontailler JY, Saugier B (1996a) Transpiration of trees and forest stands: short and long-term monitoring using sapflow methods. Global Change Biol 2:265–274

Granier A, Huc R, Barigah ST (1996b) Transpiration of natural rain forest and its dependence on climatic factors. Agric For Meteorol 78:19–29

Granville JJ (1974) Aperçu sur la structure des pneumatophores de deux espèces des sols hydromorphes en Guyane, *Mauritia flexuosa* L. et *Euterpe oleracea* Mart. (Palmae). Généralisation au système respiratoire racinare d'autres palmiers. Cah Orstom, sér Biol 23:3–22

Gribel R, Gibbs PE, Queiróz AL (1999) Flowering phenology and pollination biology of *Ceiba pentandra* in Central Amazonia. J Trop Ecol 15:247–263

Gribel R, Hay JD (1993) Pollination ecology of *Caryocar brasiliense* (Caryocaraceae) in Central Brazil cerrado vegetation. J Trop Ecol 9:199–211

Gribel R, Gibbs PE (2002) High outbreeding as a consequence of selfed ovule mortality and single vector bat pollination in the Amazonian tree *Pseudobombax munguba* (Bombacaceae). Int J Plant Sci 163(6):1035–1043

Grime JP (1989) The stress debate: symptom of impending synthesis? Biol J Linn Soc 37:3–17

Grimes A, Alarcón R, Jahnige P, Loomis S, Burnham M, Onthank K, Neill D, Palacios W, Cerón C, Balick M, Bennett B, Mendelsohn R (1994) The economic value of non-timber forest products in Ecuador. Ambio 23:405–410

Grosse W (1997) Gas transport in trees. In: Rennenberg H, Eschrich W, Ziegler H (eds) Contributions to modern tree physiology. Backhuys, Leiden

Grosse W, Armstrong J, Armstrong W (1996) A history of pressurised gas-flow studies in plants. Aquat Bot 54:87–100

Groweiss A, Cardellina JH, Boyd MR (2000) HIV-inhibitory prenylated xanthones and flavones from *Maclura tinctoria*. J Nat Prod 63:1537–1539

Grubb PJ (1998) Seeds and fruits of tropical rainforest plants: interpretation of the range in seed size, degree of defence and flesh/seeds quotients. In: Newberry DM, Purvis A, Brown S (eds) Dynamics of tropical communities. Symposium of the British Ecological Society 37, pp 1–24

Grubb PJ, Coomes DA (1997) Seed mass and nutrient content in nutrient-starved tropical rainforest in Venezuela. Seed Sci Res 7:269–280

Guariguata MR, Ostertag R (2001) Neotropical secondary succession: changes in structural and functional characteristics. Forest Ecol Manag 148:1142–1149

Guenther ACH, Erickson D, Fall R, Geron C, Graedel T, Harley P, Klinger L, Lerdau M, McKay W, Pierce T, Scholes B, Steinbrecher R, Tallamraju R, Taylor J, Zimmerman P (1995) A global model of natural volatile organic compound emission. J Geophys Res 100(D5):8873–8892

Gut A, Scheibe M, Rottenberger S, Rummel U, Welling M, Ammann A, Kirkman G, Kuhn U, Meixner FX, Kesselmeier J, Lehmann BE, Schmidt W, Miller E, Piedade MTF (2002) Exchange fluxes of the NO2 and O3 at soil and leaf surfaces in an Amazonian rain forest. J Geophys Res 107(20):1–15

Gutjahr E (1996) Untersuchungen zur Optimierung der Ackernutzung in den Überschwemmungswäldern (várzeas) am mittleren Amazonas. Studien zur Agrarökologie 21, Verlag Dr. Kovac, Kiel

Gutjahr E (2000) Prospects for arable farming in the floodplains of the Central Amazon. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers bV, Leiden, The Netherlands, pp 141–170

Haaijer SCM, Lamers LPM, Smolders AJP, Jetten MSM, op den Camp HJM (2007) Iron sulfide and pyrite as potential electron donors for microbial nitrate reduction in freshwater wetlands. Geomicrobiol J 24(5):391–401

Haase K, Rätsch G (2010) The morphology and anatomy of tree roots and their aeration strategies. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Haase K, De Simone O, Junk WJ, Schmidt W (2003) Internal oxygen transport in cuttings from flood-adapted várzea tree species. Tree Phys 23:1069–1076

Haeupler H (1983) Die Mikroarealophyten der Balearen. Ein Beitrag zum Endemismus-Begriff und zur Inselbiogeographie. Tuexenia 3:271–288

Haffer J (1969) Speciation in Amazonian forest birds. Science 165:131–137

Haffer J, Prance GT (2001) Climatic forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. Amazoniana 16:579–607

Haig D (1996) The pea and the coconut: seed size in safe sites. Tree 11:1–2

Hall JPW, Harvey D (2002) The phylogeography of Amazonia revisited: new evidence from riodinid butterflies. Evolution 56(7):1489–1497

Hamilton S, Sippel S., Calheiros D., Melack J (1999) Chemical characteristics of Pantanal waters. In: EMBRAPA (ed) Anais do II Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal, Corumbá, 1996. EMBRAPA, Corumbá, pp 89–100

Hamilton SK, Sippel SJ, Melack JM (2002) Comparison of inundation patterns among major South American floodplains. J Geophys Res – Atmos 107 (D20), art. no. 8308

Hamilton SK, Sippel SJ, Melack JM (2004) Seasonal inundation patterns in two large savanna floodplains of South America: the Llanos de Moxos (Bolivia) and the Llanos del Orinoco (Venezuela and Colombia). Hydrol Processes 18:2103–2116

Hamilton SK, Kellndorfer J, Lehner B, Tobler M (2007) Remote sensing of floodplain geomorphology as a surrogate for biodiversity in a tropical river system (Madre de Dios, Peru). Geomorphology 89:23–38

Hamrick JL, Loveless MD (1989) The genetic structure of tropical tree populations: associations with reproductive biology. In: Bock JH, Linhart YB (eds) The evolutionary biology of plants. Westview Press, Boulder, CO, pp 129–146

Hansen A-C, Steen E (1984) Methods of calculating root production and nitrogen uptake in an annual crop. Swed J Agr Res 14:191–200

Hansen MC, Fries RS, Townsend JR, Sohlberg R (2000) Global land cover classification at 1 km resolution using a classification tree approach. Int J Remote Sens 21:1331–1364

Harborne JB (1988) Introduction to ecological biochemistry, 3rd edn. London, Academic Press, p 356

Harley PC, Monson RK, Lerdou MT (1999) Ecological and evolutionary aspects of isoprene emission from plants. Oecologia 118:109–123

Harrington CA (1987) Responses of red alder and black cottonwood seedlings to flooding. Physiol Plantarum 69:35–48

Harris PP, Huntingford C, Cox PM (2008) Amazon Basin climate under global warming: the role of the sea surface temperature. Philos T Roy Soc B 363. doi:10.1098/rstb.2007.0037

Hartshorn GS (1980) Neotropical forest dynamics. Biotropica 12:23–30

Haugaasen T, Peres CA (2005) Tree phenology in adjacent Amazonian flooded and unflooded forests. Biotropica 37(4):620–630

Haugaasen T, Peres CA (2006) Floristic, edaphic, and structural characteristics of flooded and unflooded forests in the lower Rio Purús region of central Amazonia, Brazil. Acta Amazonica 36(1):25–36

Haukka K, Lindström K, Young JPW (1996) Diversity of partial 16S rRNA sequences among and within strains of African rhizobia isolated from Acacia and Prosopis. Syst Appl Microbiol 19:352–359

Haukka K, Lindström K, Young JPW (1998) Three phylogenetic groups of nodA and nifH genes in *Sinorhizobium* and *Mesorhizobium* isolates from leguminous trees growing in Africa and Latin America. Appl Environ Microbiol 64(2):419–426

Havranek WM (1981) Stammatmung, Dickenwachstum und Photosynthese einer Zirbe (*Pinus cembra* L.) an der Waldgrenze. In: Tranquillini W (ed) Radial growth in trees. Mitt. der Forstl. Bundesversuchsanstalt, Wien, 142, pp 443–467

Hayes EF, Sewlal J-AN (2004) The Amazon river as a dispersal barrier to passerine birds: effects of river width, habitat and taxonomy. J Biogeogr 31:1809–1818

Heckenberger MJ, Kuikuro A, Kuikuro UT, Russell JC, Schmidt M, Fausto C, Franchetto B (2003) Amazonia 1492: Pristine forest or cultural parkland? Science 301:1710–1713 nicht im Text

Henderson A, Galeano G, Bernal R (1995) Field guide to the palms of the Americas. Princeton University Press, New Jersey, p 351

Henderson PA, Hamilton WD, Crampton WGR (1998) Evolution and diversity in Amazonian floodplain communities. In: Newbery DM, Prins HHT, Brown ND (eds) Dynamics of tropical communities. The 37th symposium of the British ecological society, London 1998. Blackwell Science, Oxford, London, pp 385–419

Hendry GAF, Brocklebank KJ (1985) Iron-induced oxygen radical metabolism in waterlogged plants. New Phytol 101:199–206

Herforth A, Ruiz J, Mosquera E, Laux M, Rodriguez E (2003) Antifungal plants of the Peruvian Amazon: a survey of ethnomedical uses and biological activity. In: Herforth AW, Gorospe K, Kheel J, Fraissinet P, Rosane D, Rodriguez E (eds) Emanations from the Rainforest and the Caribbean, vol. 4, Cornell University

Hesmer H (1975) Leben und Werk von Dietrich Brandis, Westdeutscher Verlag

Hess LL, Melack JM (1994) Mapping wetland hydrology and vegetation with synthetic aperture radar. Internt J Ecol Environ Sci 20:197–205

Hess LL, Melack JM, Simonett DS (1990) Radar detection of flooding beneath the forest canopy: a review. Int J Remote Sens 11:1313–1325

Hess LL, Melack JM, Filoso S, Wang Y (1995) Delineation of inundated area and vegetation along the Amazon floodplain with the SIR-C synthetic aperture radar. IEEE Trans Geosci Remote Sens 33:896–904

Hess LL, Novo EMLM, Slaymaker DM, Holt J, Steffen C, Valeriano DM, Mertes LAK, Krug T, Melack JM, Gastil M, Holmes C, Hayward C (2002) Geocoded digital videography for validation of land cover mapping in the Amazon basin. Int J Remote Sens 7:1527–1556

Hess LL, Melack JM, Novo EMLM, Barbosa CCF, Gastil M (2003) Dual-season mapping of wetland inundation and vegetation for the central Amazon basin. Remote Sens Environ 87:404–428

Higuchi N, Hummel AC, Freitas JV, Malinowski JRE, Stokes R (1994) Exploração florestal nas várzeas do Estado do Amazonas: seleção de árvore, derrubada e transporte. Proceedings of the VII harvesting and transportation of timber products. IUFRO/UFPR, Curitiba, Brazil, pp 168–193

Hiraoka M (1992) Caboclo and ribereño resource management in Amazonia: a review. In: Redford H, Padoch C (eds) Conservation of neotropical forests: working fom traditional resource use. Colombia University Press, New York, pp 134–157

Hiruma-Lima CA, Calvo TR, Rodrigues CM, Andrade FD, Vilegas W, Souza Brito AR (2006) Antiulcerogenic activity of *Alchornea castaneaefolia*: effects on somatostatin, gastrin and prostaglandin. J Ethnopharmacol 104(1–2):215–224

Hoekman DH, Quiñones MJ (1998) Forest type classification by airborne SAR in the Colombian Amazon. Proceedings of the second international workshop on retrieval of bio- and geophysical parameters from SAR data for land applications, Noordwijk, The Netherlands. ESA Publications, pp 225–231

Höfer H (1997) The spider communities. In: Junk WJ (ed) The Central Amazon floodplain: ecology of a pulsing system. Ecolog Stud 126:372–384. Springer, Berlin/Heidelberg/New York

Högberg P (1990) ^{15}N natural abundance as a possible marker for the ectomycorrhizal habit of trees in mixed African woodlands. New Phytol 115:483–486

Högberg P, Piearce GP (1986) Mycorrhizas in Zambian trees in relation to host taxonomy, vegetation communities and successional patterns. J Ecol 74:775–785

Högberg P, Alexander IJ (1995) Roles of root symbioses in African woodland and forest: evidence from ^{15}N abundance and foliar analysis. J Ecol 83:217–224

Holmes TP, Blate GM, Zweede JC, Pereira R, Barreto P, Boltz F, Bauch R (2002) Financial and ecological indicators of reduced impact logging performance in the eastern Amazon. Forest Ecol Manag 163:93–110

Hölscher D, Koch O, Korn S, Leuschner C (2005) Sap flux of five co-occurring tree species in a temperate broad-leaved forest during seasonal soil drought. Trees 19:628–637

Holzinger R, Sandoval-Soto L, Rottenberger S, Crutzen PJ, Kesselmeier J (2000) Emissions of volatile organic compounds from Quercus ilex L. measured by Proton transfer reaction mass spectrometry under different environmental conditions. J Geophys Res -Atmos 105(D16):20/573–579

Homma AKO (1998) A civilização da juta na Amazônia: expansão e declínio. In: Homma AKO (ed) Amazônia: mei ambiente e desnvolivmento agricola. EMBRAPA, Belém, Brasil, pp 33–60

Hook DD (1984) Adaptations to flooding with fresh water. In: Kozlowski TT (ed) Flooding and plant growth. Academic Press, Orlando, FL, pp 265–294

Hook DD, Brown CL, Kormanik PP (1970) Lenticel and water root development of swamp tupelo under various flooding conditions. Bot Gaz 131(3):217–224

Hopf M, Münchow G (2000) Diseases of Cattel and Water Buffalo in the Central Amazon floodplain. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers bV, Leiden, The Netherlands, pp 345–373

Hormaetxe K, Esteban R, Becerril JM, García-Plazaola JI (2005) Dynamics of the α-tocopherol pool as affected by external (environmental) and internal (leaf age) factors in *Buxus sempervirens* leaves. Physiologia Plantarum 125:333–344

Horn MH (1997) Evidence for dispersal of fig seeds by the fruit-eating charachid fish *Brycon guatemalensis* Regan in a Costa Rican tropical rain forest. Oecologia 109:259–264

Horna V (2001) Carbon release from woody parts of trees of a seasonally flooded Amazon forest near Manaus, Brazil. Unpublished Ph.D. thesis, Department of Plant Ecology, University of Bayreuth

Horna V (2002) Carbon release from woody parts of trees from a seasonally flooded Amazon forest near Manaus, Brasil. Bayreuther Forum Ökologie 94:1–137

Horna V, Zimmermann R, Müller E, Parolin P (2010) Sap flow and stem respiration. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Hose E, Clarkson DT, Steudle E, Schreiber L, Hartung W (2001) The exodermis: a variable apoplastic barrier. J Exp Bot 52(365):2245–2264

Houghton RA, Skole DL, Nobre CA, Hackler JL, Lawrence KT, Chomentowski WH (2000) Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. Nature 403:301–304

Hubbell SP (1995) Towards a theory of biodiversity and biogeography of continuous landscapes. In: Carmichael GR, Folk GE, Schnoor JL (eds) Preparing for global change: a midwestern perpspective. SPB Academic Publishing, The Hague, pp 171–199

Hubbell SP, Foster RB (1986) Biology, chance, and history and the structure of tropical rain forest tree communities. In: Diamond J, Case DJ (eds) Community ecology. Harper & Row, New York, pp 314–330

Hubbell SP, Foster RB (1992) Short-term dynamics of a neotropical forest: why ecological reserach matters to tropical conservation and management. Oikos 63:48–61

Huber J (1910) Matas e madeiras amazônicas. Boletim do Museo Goeldi Belém 6:91–203

Huber O (1982) Significance of savanna vegetation in the Amazon territory of Venezuela. In: Prance GT (ed) Biological diversification in the tropics. Columbia University Press, New York, pp 221–244

Hueck K (1966) Die Wälder Südamerikas. Gustav Fischer Verlag, Stuttgart, pp 422

Hummel AC (1994) Diagnóstico do subsetor madeirerio do Estado do Amazonas. Série Estudos Setoriais. Edição Sebrae, Manaus, Brazil

Hund M, Ohly JJ (2000) Permanent crop cultivation on central Amazonian floodplains. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers bV, Leiden, The Netherlands, pp 191–213

Husseein AA, Bozzi B, Correa M, Capson TL, Kursar TA, Coley PD, Solis PN, Gupta MP (2003) Bioactive constituents from three *Vismia* species. J Nat Prod 66(6):858–860

Huth A, Ditzer T (2000) Simulation of the growth of a lowland Dipterocarp rain forest with FORMIX3. Ecol Model 134:1–25

Huth A, Drechsler M, Köhler P (2005) Using multicriteria decision analysis and a forest growth model to assess impacts of tree harvesting in Dipterocarp lowland rainforests. Forest Ecol Manag 207:215–232

Hutyra LR, Munger JW, Nobre CA, Saleska SR, Vieira SA, Wofsy SC (2005) Climatic variability and vegetation vulnerability in Amazonia. Geophys Res Lett 32:1–4

IBAMA (1994) Relatório preliminar sobre ordenamento pesqueiro para a bacia Amazônica. IBAMA, relatório técnico, Brasilia, Brazil

IBAMA (1997) Administração participativa: um desafio à gestão ambiental.- IBAMA, relatório técnico, Brasilia, Brazil

IBAMA (2000) Projeto de manejo dos recursos naturais das várzeas. Manaus, p 64

IEB (2007) Diagnóstico retrata a situação dos planos de manejo florestal comunitário e de pequena escala na Amazônia brasileira.T TInstituto Internacional de Educação do Brasil – IEB. http://www.iieb.org.br/diagnosticomfc/diagnostico_am.html

Ihering RV, Azevedo P (1934) A curimatá dos açudes nordestinos (*Prochilodus argenteus*). Arq Inst Biol São Paulo 5:142–184

Ihering RV, Azevedo P (1936) A desova e a hipofisação dos peixes. Evolução de dois Nomatognatas. Arq Inst Biol São Paulo 7:107–118

Ilhardt BL, Verry ES, Palik BJ (2000) Defining riparian areas. In: Verry ES, Hornbeck JW, Dolloff CA (eds) Riparian management in forests of the continental eastern United States. Lewis Publishers, Boca Raton/London/New York/Washington DC, pp 23–42

INPE (2006) Monitoramento da floresta amazônica brasileira por satélite. Instituto Nacional de Pesquisas Espaciais (INPE), São José dos Campos, Brazil. http://www.obt.inpe.br/prodes/index.html

Insalud N, Bell RW, Colmer TD, Rerkasem B (2006) Morphological and pysiological rsponses of rice (*Oryza sativa*) to limited phosphorous supply in aerated and stagnant solution culture. Ann Bot 98:995–1004

Insausti P, Grimoldi AA, Chaneton EJ, Vasellati V (2001) Flooding induces a suite of adaptive plastic responses in the grass *Paspalum dilatatum*. New Phytol 152:291–299

Inuma JJ (2006) Comparação na diversidade e estrutura das comunidades de plantas lenhosas da terra firme, várzea e igapó do Amaná, Amazônia Central. Ph.d.-Thesys, Instituto Nacional de Pesquisas da Amazônia, Manaus

IPCC (2007) Climate change 2007: the physical science basis: summary for policymakers and technical summary. Working group I of the intergovernmental panel on climate change (IPCC), WMO & UNEP, Geneva, Switzerland

Irion G (1976a) Quarternary sediments of the upper Amazon lowlands of Brazil. Biogeographica 7:163–167

Irion G (1976b) Mineralogisch-geochemische Untersuchungen an der pelitischen Fraktion amazonischer Oberböden und Sedimente. Biogeographica 7:7–25

Irion G (1978) Soil infertility in the Amazonian rain forest. Naturwissenschaften 65:515–519

Irion G (1984a) Clay minerals of Amazon soils. In: Sioli H (ed) The Amazon – limnology and landscape ecology of a mighty tropical river and its Basin, pp 537–579. The Hague, Boston, Lancaster (Dr. W. Junk)

Irion G (1984b) Sedimentation and sediments of Amazon rivers and evolution of the Amazon landscape since Pliocene times. In: Sioli H (ed) The Amazon – limnology and landscape ecology of a mighty tropical river and its Basin, pp 201–214. The Hague, Boston, Lancaster (Dr. W. Junk)

Irion G, Adis J, Junk W, Wunderlich F (1984) Sedimentaufbau einer Amazonas-Insel. Natur und Museum 114(1):1–13

Irion G, Junk WJ (1989) Amazonian lake sediments. In: XXIVth Congress of the international association of theoretical and applied limnology, 13–19 August 1989, vol 69, München (Abstract)

Irion G, Müller J, Nunes de Mello J, Junk WJ (1995) Quarternary geology of the Amazonian lowland. Geo-Mar Lett 15:172–178

Irion G, Junk WJ, Mello JASN (1997) The large Central Amazonian river floodplains near Manaus: geological, climatological, hydrological, and geomorphological aspects. In: Junk WJ (ed) The Central Amazon floodplains. Ecology of a pulsing system. Springer, Berlin/Heidelberg/New York, pp 23–46

Irion G, Mueller J, Keim G, Nunes De Mello J, Junk WJ (1999) The late quaternary river and lake development in Central Amazonia. Extended abstract (10 pages) in the Abstract-Volume (CD-ROM) of the international symposium on Hydrological and geochemical processes in large-scale river basins, Manaus/Brazil

Irion G, Bush MB, Nunes de Mello JA, Stüben D, Neumann T, Müller G, de Morais JO, Junk JWA (2006) Multiproxy record of Holocene lake sediments from the Rio Tapajós, eastern Amazonia. Palaeogeograph Palaeoclimatol Palaeoecol 240:523–535

Irion G, de Mello JASN, Morais J, Piedade MTF, Junk WJ, Garming L (2010) Development of the Amazon valley during the middle to late quaternary: sedimentological and climatological observations. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Irmler U (1977) Inundation–forest types in the vicinity of Manaus. Biogeographica 8:17–29

Isaac VJ, Ruffino ML, McGrath D (1998) In search of a new approach to fisheries management in the middle Amazon. In: Quinn II TJ, Funk F, Heifetz J, Ianelli J, Power J, Schweigert J, Sullivan P, Zhang CI (eds) Fishery stock assessment model. Alaska Sea Grant College Program, University of Alaska, Fairbanks, AS-SG-98-01, pp 889–902

Ishima IH (1998) Estudos dendrocronológicos e determinação da idade de árvores das matas ciliares do Pantanal Sul-Matogrossense. Dissertation, Universidade Federal de São Carlos, São Carlos

Jackson MB, Armstrong W (1999) Formation of aerenchyma and the process of plant ventilation in relation to soil flooding and submergence. Plant Biol 1:274–287

Jackson MB, Colmer TD (2005) Response and adaptation by plants to flooding stress. Ann Bot 96:501–505

Jackson RM, Mason PA (1984) Mycorrhiza. The institute of biology's studies in biology, p 59. E Arnold Publications, London

Janos DP (1983) Tropical mycorrhizas, nutrient cycles and plant growth. In: Sutton SL, Whitemore TC, Chadwick AC (eds) Tropical rain forest: ecology and management. Blackwell Scientific, Oxford, pp 327–345

Jansen M, Martin P-G (1995) Anwendung des Bestandessimulationsmodells TREEDYN3 auf die Fichten-Versuchsfläche Solling F1. Ber Forschz Waldökos Reihe B 45:1–79

Janzen DH (1967) Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21:620–637

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Amer Nat 104:501–528

Janzen DH (1974) Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. Biotropica 6:69–103

Janzen DH (2003) How polyphagous are Costa Rican forest saturniid caterpillars? In: Basset, Y., Novotny, V., Miller, S.E. & R.L. Kitching (eds) Arthropods of tropical forests. Spatio-temporal dynamics and resource use in the canopy, pp 369–379. Cambridge University Press, Cambridge, p 474

Jaramillo CA, Dilcher DL (2000) Microfloral diversity patterns of the late Paleocene-Eocene interval in Colombia, northern South America. Geology 28:815–818

Jaramillo CA, Dilcher DL (2001) Middle paleogene palynology of central Colombia, South America: a study of pollen and spores from tropical latitudes. Palaeontograph Abt B 258:87–213

Jetten MSM, Strous M, van de Pas-Schoonen K, Schalk J, van Dongen UGJM, van den Graaf AA, Logemann S, Muyzer G, van Loosdrecht MCM, Kuenen JG (1999) The anaerobic oxidation of ammonium. FEMS Microbiol Rev 22:421–437

Johns JS, Baretto P, Uhl C (1996) Logging damage during planned and unplanned logging operations in the eastern Amazon. Forest Ecol Manag 89:59–77

Johnson KR, Ellis B (2002) A tropical rainforest in Colorado 1.4 million years after the Cretaceous-tertiary boundary. Science 296:2379–2383

Johnson RL, Little EL (1967) Trees, shrubs and woody vines of the Bluff experimental forest, Warren County, Mississippi. US Forest Service research paper 26, New Orleans

Johnson WC, Burgress RL, Keammerer WR (1976) Forest overstay vegetation end environment on the Missouri river floodplain in North Dakota. Ecol Monogr 46:59–84

Joly CA (1991) Flooding tolerance in tropical trees. In: Jackson MB, Davies DD, Lambers H (eds) Plant life under oxygen deprivation. SPB Academic Publishing bV, The Hague, pp 23–34

Joly CA (1996) The role of oxygen diffusion to the root system on the flooding tolerance of tropical trees. Rev Brasil Biol 56(2):375–382

Joly CA, Crawford RMM (1982) Variation in tolerance and metabolic responses to flooding in some tropical trees. J Experiment Bot 33:799–809

Jordan C, Caskey W, Escalante G, Herrera R, Montagnini F, Todd R, Uhl C (1983) Nitrogen dynamics during conversion of primary Amazonian rain forest to slash and burn agriculture. Oikos 40:131–139

Jordan CF (1983) Productivity of tropical rain forest ecosystems and the implication for their use as future wood and energy resources. In: Golley FB (ed) Tropical rain forest ecosystems. Ecosystems of the World 14 A. Elsevier, Amsterdam, pp 117–136

Jordan DC (1984) Family III. Rhizobiaceae Conn 1938, 321^{AL}. In: Krieg NR, Holt JC (eds) Bergey's manual of systematic bacteriology. Williams & Wilkins, Baltimore 1:234–254

Josse C, Navarro G, Encarnación F, Tovar A, Comer P, Ferreira W, Rodríguez F, Saito J, Sanjurjo J, Dyson J, Rubin de Celis E, Zárate R, Chang J, Ahuite M, Vargas C, Paredes F, Castro W, Maco J, Reátegui F (2007) Ecological systems of the Amazon basin of Peru and Bolivia: classification and Mapping. NatureServe, Arlington, Virginia, USA

Julliot C (1996) Seed dispersal by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. Int J Primatol 17:239–258

Junk WJ (1980) Áreas inundáveis - um desafio para limnologia. Acta Amazonica 10(4):775–795

Junk WJ (1983) Ecology of swamps in the Middle Amazon. In: Gore AJP (ed) Ecosystems of the world. Mires: Swamp, Bog, Fen and Moor, B. Regional Studies. Elsevier, Amsterdam, pp 269–294

Junk WJ (1984) Ecology of the várzea, floodplain of Amazonian white water rivers. In: Sioli H (ed) The Amazon – limnology and landscape ecology of a mighty tropical river and its basin. Monographiae Biologicae. Junk Publications, Dordrecht, pp 216–243

Junk WJ (1985) The Amazon floodplain – a sink or a source of organic carbon? In: Degin ET, Kempe S, Herrera R (eds) Transport of carbon in the major World rivers. Part 3. Mitt Geol-Paläont Inst 58:267–283

Junk WJ (1989) Flood tolerance and tree distribution in central Amazonian floodplains. In: Holm-Nielsen LB, Nielsen IC, Balslev H (eds) Tropical forests: botanical dynamics, speciation and diversity. Academic Press, New York, pp 47–64

Junk WJ (1993) Wetlands of tropical South America. In: Whigham D, Hejny S, Dykyjova D (eds) Wetlands of the world. Junk Publications, Dordrecht, pp 679–739

Junk WJ (ed) (1997a) The Central Amazon floodplains. Ecology of a pulsing system. Springer, Berlin/Heidelberg/New York, pp 525

Junk WJ (1997b) General aspects of floodplain ecology with special reference to Amazonian floodplains. In: Junk WJ (ed) The Central Amazon floodplain: ecology of a pulsing system. Ecolog Studies 126:3–20. Springer, Berlin/Heidelberg/New York

Junk WJ (2000a) The Central Amazon river floodplain: concepts for the sustainable use of its resources. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers bV, Leiden, pp 75–94

Junk WJ (2000b) Mechanisms for development and maintenance of biodiversity in neotropical floodplains. In: Gopal B, Junk WJ, Davis JA (eds) Biodiversity in wetlands: assessment, function and conservation, vol 1, Backhuys Publishers. Leiden, The Netherlands, pp 119–139

Junk WJ (2002) Long-term environmental trends and the future of tropical wetlands. Environ Conserv 29(4):414–435

Junk WJ (2005) Flood pulsing and the linkages between terrestrial, aquatic, and wetland systems. Verh Int Ver Theor Angew Limnol 29(1):11–38

Junk WJ, Furch K (1985) The physical and chemical properties of Amazonian waters and their relationship with the biota. In: Prance GT, Lovejoy T (eds) Amazonia: key environments. Pergamon Press, Oxford, pp 3–17

Junk WJ, Barley PB, Sparks RE (1989) The flood-pulse concept in river-floodplain systems. Can Spec Publ Fish Aquat Sci 106:110–127

Junk WJ, Welcomme RL (1990) Floodplains In: Patten BC et al (eds) Wetlands and shallow continental water bodies, vol 1. SPB Academic Publishing, Netherlands, pp 491–524

Junk WJ, Furch K (1993) A general review of tropical South American floodplains. Wetlands Ecol Manage 2:231–238

Junk WJ, Piedade MTF (1993) Herbaceous plants in the floodplain near Manaus: species diversity and adaptations to the flood pulse. Amazoniana 12:467–484

Junk WJ, Piedade MTF (1997) Plant life in the floodplain with special reference to herbaceous plants. In: Junk WJ (ed) The central Amazon floodplain: ecology of a pulsating system. Ecolog Stud 126:147–186. Springer, Berlin/Heidelberg/New York

Junk WJ, Soares MGM, Saint-Paul U (1997) The fish. In: Junk WJ (ed) The Central Amazon floodplain – ecology of a pulsing system. Springer, Berlin. Ecolog Stud 126:385–408

Junk WJ, Ohly JJ (eds.) (2000) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers, Leiden, The Netherlands

Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) (2000a) The central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers b.V, Leiden

Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (2000b) Actual use and options for the sustainable management of the central Amazon floodplain: discussion and conclusions. In: Junk WJ, Ohly

JJ, Piedade MTF, Soares MGM (eds) The central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers b.V, Leiden, pp 535–579

Junk WJ, Wantzen KM (2004) The flood pulse concept: new aspects, approaches, and applications – an update. In: Welcomme RL, Petr T (eds) Proceedings of the second international symposium on the management of large rivers for fisheries, vol 2. Food and agriculture organization & Mekong River commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/16, pp 117–149

Junk WJ, Piedade MTF (2004) Status of knowledge, ongoing research, and research needs in Amazonian wetlands. Wetlands Ecol Manage 12:597–609

Junk WJ, Piedade MTF (2005) Amazonian wetlands. In: Fraser LH, Keddy PA (eds) Large wetlands: their ecology and conservation. Cambridge University Press, Cambridge, pp 63–117

Junk WJ, Nunes da Cunha C, Wantzen KM, Petermann P, Strüssmann C, Marques MI, Adis J (2006) Comparative biodiversity value of large wetlands: the Pantanal of Mato Grosso, Brazil. Aquat Sci 68:278–309

Junk WJ, Soares MG, Bayley PB (2007) Freshwater fishes of the Amazon River basin: their biodiversity, fisheries and habitats. Aquat Ecosyst Health Manage 10(2):153–173

Junk WJ, Bayley PB (2008) The scope of the flood pulse concept regarding riverine fish and fisheries, given geographic and man-made differences among systems. Am Fish Soc Sympo 49:907–1923

Junk WJ, Piedade MTF (2010) An introduction to SouthAmerican wetland forests: distribution, definitions and general characterization. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Junk WJ, Piedade MTF, Wittmann F, Schöngart J (2010a) The role of floodplain forests in an integrated sustainable management concept of the natural resources of the central Amazonian várzea. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Junk WJ, Piedade MTF, Parolin P, Wittmann F, Schöngart J (2010b) Ecophysiology, biodiversity and sustainable management of central Amazonian floodplain forests: a synthesis. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Justi KC, Visentainer JV, Evelazio de Souza N, Matsushita M (2000) Nutritional composition and Vitamin C stability in stored camu-camu (*Myrciaria dubia*) pulp. Arch Latinoam Nutr 50(4):405–408

Justin SHFW, Armstrong W (1987) The anatomical characteristics of roots and plant response to soil flooding. New Phytol 106:465–495

Kahn F, Henderson A (1999) An overview of the palms of the várzea in the Amazon region. In: Padoch C, Ayres M, Pinedo-Vasquez M, Henderson A (eds) Várzea: diversity, development, and conservation of Amazonia's whitewater floodplains. New York Botanical Garden Press, New York, pp 187–193

Kahn F, Mejia K (1990) Palm communities in wetland forest ecosystems of Peruvian Amazonia. Forest Ecol Manage 33(34):169–179

Kalliola R, Salo J, Puhakka M, Rajasilta M (1991) New site formation and colonizing vegetation in primary succession on the western Amazon floodplains. J Ecol 79:877–901

Kalliola R, Salo J, Puhakka M, Rajasilta M, Häme T, Neller RJ, Räsänen ME, Danjoy Arias WA (1992) Upper Amazon channel migration. Naturwissenschaften 79:75–79

Kalliola R, Puhakka M, Danjoy W (1993) Amazonia Peruana – Vegetacion humeda tropical en el llano subandino. Gummerus Printing, Jyväskylä

Kammesheidt L, Köhler P, Huth A (2001) Sustainable timber harvesting in Venezuela: a modelling approach. J Appl Ecol 38:756–770

Kammesheidt L, Dagang AA, Schwarzwäller W, Weidelt H-J (2003) Growth patterns of dipterocarps in treated and untreated plots. Forest Ecol Manag 174:437–445

Kasischke ES, Melack JM, Dobson MC (1997) The use of imaging radar for ecological applications-a review. Remote Sens Environ 59:141–156

Kawase M, Whitmoyer RE (1980) Aerenchyma development in waterlogged plants. Am J Bot 67(1):18–22

Keel SHK, Prance GT (1979) Studies of the vegetation of a white-sand black-water igapó (Rio Negro, Brazil). Acta Amazonica 9:645–655

Keim G, Irion G, Behling H, Junk WJ, Nunes De Mello J (1999) The sediment deposits of Lago Calado, a Ria Lake in Central Amazonia (Brazil), as indicator for postglacial water level rise of the Amazon river. Extended abstract (8 pages) in the Abstact-Volume (CD-ROM) of the international symposium on Hydrological and geochemical processes in large-scale river basins, Manaus/Brazil

Keller M, Palace M, Hurtt G (2001) Biomass estimation in the Tapajos National Forest, Brazil – examination of sampling and allometric uncertainties. Forest Ecol Manag 154:371–382

Kellman M, Tackaberry R, Brokaw N, Meave J (1994) Tropical gallery forests. Natl Geo Res Explor 10(1):92–103

Kelly CK (1995) Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. Oecologia 102:377–388

Kern J (1995) Die Bedeutung der N_2-Fixierung und der Denitrifikation für den Stickstoffhaushalt des amazonischen Überschwemmungssees Lago Camaleão. Ph.D. thesis, University of Hamburg, pp 178

Kern J, Darwich A (1997) Nitrogen turnover in the várzea. In: Junk WJ (ed) The Central Amazon floodplains. Ecology of a pulsing system. Springer, Berlin/Heidelberg/New York, pp 119–135

Kern J, Darwich A (2003) The role of periphytic N_2 fixation for stands of macrophytes in the whitewater floodplain (Várzea). Amazoniana 17:361–375

Kern J, Darwich A, Furch K, Junk WJ (1996) Seasonal denitrification in flooded and exposed sediments from the Amazon floodplain at Lago Camaleão. Microb Ecol 32:47–57

Kern J, Darwich A, Förstel H (2000) Studies on the role of N_2 fixation in the floodplain forest in the Central Amazon. Verh Internat Verein Limnol 27:610–614

Kern J, Kreibich H, Koschorreck M, Darwich A (2010) Nitrogen balance of a floodplain forest of the Amazon River: the role of Nitrogen fixation. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Kesselmeier J (2001) Exchange of short-chain oxygenated volatile organic compounds (VOCs) between plants and the atmosphere: a compilation of field and laboratory studies. J Atmosph Chemis 39(3):219–233

Kesselmeier J, Bode K, Hofmann U, Müller H, Schäfer L, Wolf A, Ciccioli P, Brancaleoni E, Cecinato A, Frattoni M, Foster P, Ferrari C, Jacob V, Fugit JL, Dutaur L, Simon V, Torres L (1997) Emission of short chained organic acids, aldehydes and monoterpenes from Quercus ilex L. and Pinus pinea L. in relation to physiological activities, carbon budget and emission algorithms. Atmos Environ 31(SI):119–134

Kesselmeier J, Staudt M (1999) Biogenic volatile organic compounds (VOC): an overview on emission, physiology and ecology. J Atmos Chem 33:23–88

Kesselmeier J, Ciccioli P, Kuhn U, Stefani P, Biesenthal T, Rottenberger S, Wolf A, Vitullo M, Valentini R, Nobre AD, Kabat P, Andreae MO (2002) Volatile organic compound emissions in relation to plant carbon fixation and the terrestrial carbon budget. Global Biogeochem Cy 16(4):1126. DOI:10.1029/2001GB001813

Ketterings QM, Coe R, Van Noordwijk M, Ambagau Y, Palm CA (2001) Reducing uncertainty in the use of allometric biomass equations for predicting above-ground biomass in mixed secondary forests. Forest Ecol Manag 146:199–209

Kimmerer TW, Kozlowski TT (1982) Ethylene, ethane, acetaldehyde, and ethanol production by plants under stress. Plant Physiol 69:840–847

Kimmerer TW, MacDonald RC (1987) Acetaldehyde and ethanol biosynthesis in leaves of plants. Plant Physiol 84:1204–1209

Kirmse S, Adis J, Morawetz W (2003) Flowering events and beetle diversity in Venezuela. In: Basset Y, Novotny V, Miller SE, Kitching RL (eds) Arthropods of tropical forests. Spatio-temporal dynamics and resource use in the canopy, pp 256–265. Cambridge University Press, Cambridge, p 474

Klenke M, Ohly JJ (1993) Wood from floodplains. In: Junk WJ, Bianchi HK (eds) 1st shift workshop, Belém, 1993. GKSS-Research Center, Geesthacht

Klinge H (1973) Root mass estimation in lowland tropical rain forests of Central Amazon, Brazil. I. Fine root masses of a pale yellow latosol and a giant humus podzol. Trop Ecol 14(1):29–38

Klinge H (1978a) Litter production in tropical ecosystems. Malayan Nat J 30(2):415–422

Klinge H (1978b) Studies on the ecology of Amazon Caatinga in soutern Venezuela. Acta Cient Venez 29:258–262

Klinge H, Ohle W (1964) Chemical properties of rivers in the Amazonian area in relation to soil conditions. Verh Int Ver Limn XV:1067–1076

Klinge H, Rodrigues WA (1968) Litter production in an area of Amazonian terra firme forest. Part I. Litter-fall, organic carbon and total nitrogen contents of litter. Amazoniana I(4):287–302

Klinge H, Rodrigues WA, Bruenig E, Fittkau EJ (1975) Biomass and structure in a Central Amazonian forest. In: Golley FB, Medina E (eds) Trends in terrestrial and aquatic research. Springer, New York, pp 115–122

Klinge H, Medina E, Herrera R (1977) Studies on the ecology of Amazon Caatinga forest in southern Venezuela. Acta Cient Venez 28:270–276

Klinge H, Medina E (1979) Rio Negro caatingas and campinas, Amazonas States of Venezuela and Brazil. In: Specht RL (ed) Heathlands and related shrublands. Descriptive studies. Ecosystems of the World, vol 9A. Elsevier, Amsterdam, pp 483–488

Klinge H, Herrera R (1983) Phytomass structure of natural plant communities on spodosols in southern Venezuela: the tall Amazon Caatinga forest. Vegetatio 53:65–84

Klinge H, Furch K, Harms E, Revilla J (1983) Foliar nutrient levels of native tree species from central Amazonia. 1 Inundation forests. Amazoniana 8:19–45

Klinge H, Junk WJ, Revilla CJ (1990) Status and distribution of forested wetlands in tropical South America. Forest Ecol Manage 33/34:81–101. Elsevier, Amsterdam

Klinge H, Adis J, Worbes M (1996) The vegetation of a seasonal várzea forest in the lower Solimões River, Amazon region of Brazil. Acta Amazonica 25(3–4):201–220

Klok EJ, Wilson IW, Wilson D, Chapman SC, Ewing RM, Somerville SC, Peacock WJ, Doferus R, Dennis ES (2002) Expression profile analysis of the low-oxygen response in Arabidopsis root cultures. Plant Cell 14:2481–2494

Kochmer JP, Handel SN (1986) Constraints and competition in the evolution of flowering phenology. Ecol Monograph 56:303–325

Kohlhepp G (1989) Verkehrs-, Siedlungs- und Wirtschaftsentwicklung und Probleme der regionalen Entwicklungsplanung im brasilianischen Amazonien. In: Hartmann G (ed) Amazonien im Umbruch: symposium über aktuelle Probleme und deutsche Forschungen im größten Regenwaldgebiet der Erde. Dietrich Reimer Verlag, Berlin, pp 123–140

Komiyama A, Ogino K, Aksonkoae S, Sabhasri S (1987) Root biomass of a mangrove forest in southern Thailand. 1. Estimation by the trench method and the zonal structure of root biomass. J Trop Ecol 3:97–108

Končalová H (1990) Anatomical adaptations to waterlogging in roots of wetland graminoids: limitations and drawbacks. Aqu Bot 38:127–134

Korning J, Balslev H (1994) Growth rates and mortality patterns of tropical lowland tree species and the relation to forest structure in Amazonian Ecuador. J Trop Ecol 10:151–166

Koschorreck M (2005) Nitrogen turnover in drying sediments of an Amazon floodplain lake. Microb Ecol 49:567–577

Koschorreck M, Darwich A (2003) Nitrogen dynamics in seasonally flooded soils in the Amazon floodplain. Wetlands Ecol Manage 11:317–330

Koshikene D (2005) Estratégias germinativas de sete espécies florestais de diferentes estágios sucessionais da várzea na Amazônia Central. Unpublished Master Thesis, pp 74

Kosuth et al (2001) www.ana.gov.br/hibam/bancodedados/Br.22.pdf

Kottke I (1986) Wurzelentwicklung und Wachstum der Fichte (Picea abies L.H. Karsten) auf unterschiedlichen Böden und künstlichen Substraten. In: Einsele G (ed) Das landschaftsökologische Forschungsprojekt Naturpark Schönbuch. Wasser- und Stoffhaushalt, Bio- Geo- und Forstwirtschaftliche Studien in Südwestdeutschland, VCH, Weinheim, pp 443–462

Kotzias D, Konidari C, Sparta C (1997) Volatile carbonyl compounds of biogenic origin – emission and concentration in the atmosphere. In: Helas G, Slanina J, Steinbrecher R (eds) Biogenic volatile organic Carbon compounds in the atmosphere. SPB Academic Publishing, Amsterdam, pp 67–78

Kozlowski TT (1984a) Plant response to flooding of soil. BioScience 34(3):162–167

Kozlowski TT (1984b) Responses of woody plants to flooding. Flooding and plant growth. Academic Press, Orlando, FL, pp 129–163

Kozlowski TT (1997) Responses of woody plants to flooding and salinity. Tree Physiol Monograph 1:1–29

Kozlowski TT (2002) Physiological ecology of natural regeneration of harvested and disturbed forest stands: implications for forest management. For Ecol Manage 158:195–221

Kozlowski TT, Pallardy SG (1997) Growth control in woody plants. Academic Press, San Diego, p 410

Krack S (2000) Untersuchungen zur Überflutungstoleranz von Bäumen (Jungpflanzen) der zentralamazonischen Weisswasser-Überschwemmungswälder (várzea) bei Manaus, Amazonas. Universität Würzburg, Master-Diss

Kraus CM, Neszmelyi A, Holly S, Wiedemann B, Nenninger A, Torssell KB, Bohlin L, Wagner H (1998) New acetylenes isolated from the bark of *Heisteria acuminata*. J Nat Prod 61(4):422–427

Kreibich H (2002) N2 fixation and denitrification in a floodplain forest in Central Amazonia, Brazil. Forschungsbericht Agrartechnik – VDI-MEG no. 398

Kreibich H, Kern J (2003) Nitrogen fixation and denitrification in a floodplain forest near Manaus, Brazil. Hydrolog Process 17:1431–1441

Kreibich H, Kern J (2004) Forest biological resources in the Amazon basin. In: Werner D (ed) Biological resources and migration. Springer, Berlin/Heidelberg, pp 83–92

Kreibich H, Lehmann J, Scheufele G, Kern J (2003) Nitrogen availability and leaching during the terrestrial phase in a várzea forest of the Central Amazon floodplain. Biol Fert Soils 39:62–64

Kreibich H, Kern J, de Camargo PB, Moreira MZ, Victória RL, Werner D (2006) Estimation of symbiotic N_2 fixation in an Amazon floodplain forest. Oecologia 147(2):359–368

Kreuzwieser J, Kühnemann F, Martis A, Rennenberg H, Urban W (2000) Diurnal pattern of acetaldehyde emission by flooded poplar trees. Physiol Plant 108:79–86

Kreuzwieser J, Scheerer U, Rennenberg H (1999) Metabolic origin of acetaldehyde emitted by poplar (Populus tremula x P-alba) trees. J Exp Bot 50(335):757–765

Kubitzki K (1985a) The dispersal of forest plants. In: Prance GT, Lovejoy TE (eds) Amazonia – key environments. Pergamon, Oxford, pp 129–163

Kubitzki K (1985b) Ichthyochory in *Gnetum venosum*. An Acad Brasil Cienc 57:513–516

Kubitzki K (1989a) The ecogeographical differentiation of Amazonian inundation forests. Plant Syst Evol 162:285–304

Kubitzki K (1989b) Amazonas-Tiefland und Guayana-Hochland – historische und ökologische Aspekte der Florenentwicklung. Amazoniana 11:1–12

Kubitzki K (1989c) Die Flora der amazonischen Überschwemmungswälder und ihre ökologischen Beziehungen. In: Hartmann G (ed) Amazonien im Umbruch. Dietrich Reimer Verlag, pp 215–226

Kubitzki K (1991) Dispersal and distribution in *Leopoldinia* (Palmae). Nord J Bot 11:429–432

Kubitzki K, Ziburski A (1994) Seed dispersal in floodplain forest of Amazonia. Biotropica 26(1):30–43

Kvist LP, Nebel G (2001) A review of Peruvian flood plain forests: ecosystems, inhabitants and resource use. Forest Ecol Manage 150:3–26

Kvist LP, Andersen MK, Stagegaard J, Hesselsøe M, Llapapasca C (2001) Extraction from woody forest plants in flood plain communities in Amazonian Peru: use, choice, evaluation and conservation status of resources. Forest Ecol Manag 150:147–174

Kyparissis A, Petropoulou Y, Manetas Y (1995) Summer survival of leaves in a soft-leaved shrub (*Phlomis fruticosa* L, Labiatae) under Mediterranean field conditions: avoidance of photoinhibitory damage through decreased chlorophyll contents. J Exp Bot 46(293):1825–1831

Laan P, Blom CWPM (1990) Growth and survivial responses of *Rumex* species to flooded and submerged conditions: the importance of shoot elongation, under-water photosynthesis and reserve carbohydrates. J Exp Bot 41:775–783

Lacerda LD, Conde JE, Kjerfve B, Alvarez-León R, Alarcón A, Polanía J (2002) American Mangroves. In: Lacerda LD (ed) Mangrove ecosystems. Function and management. Springer, Berlin/Heidelberg/New York, pp 1–62

Laclau JP, Toutain F, M'Bou AT, Arnoud M, Joffre R, Ranger J (2004) The function of the superficial root mat in the biochemical cycles of nutrients in Congolese Eucalyptus plantations. Ann Bot 93:249–261

Lafay B, Burdon JJ (1998) Molecular diversity of rhizobia occurring on native shrubby legumes in southeastern Australia. Appl Environ Microbiol 64(10):3989–3997

Lambert JE, Garber PA (1998) Evolutionary and ecological implications of primate seed dispersal. Am J Primatol 45:9–28

Lamotte S (1990) Fluvial dynamics and succession in the lower Ucayali River basin, Peruvian Amazonia. Forest Ecol Manage 33(34):141–156

Lamprecht H (1986) Waldbau in den Tropen: Die tropischen Waldökosysteme und ihre Baumarten – Möglichkeiten und Methoden zu ihrer nachhaltigen Nutzung. Paul Parey, Hamburg, p 318

Lamprecht H (1989) Silviculture in the tropics: tropical forest ecosystems and their tree species – possibilities and methods for their long-term utilization. GTZ, Eschborn

Larcher W (1994) Ökophysiologie der Pflanzen: Leben, Leistung und Streßbewältigung der Pflanzen in ihrer Umwelt. 5 Aufl Ulmer Stuttgart, UTB für Wissenschaft 394 S

Latrubesse EM, Franzinelle E (2002) The Holocene alluvial plain of the middle Amazon River, Brazil. Geomorphology 44:241–257

Laurance WF, Fearnside PM, Laurance SG, Delamonica P, Lovejoy TE, Rankin-de-Merona JM, Chambers JQ, Gascon C (1999) Relationship between soils and Amazon forest biomass: a landscape-scale study. Forest Ecol Manag 118:127–138

Laurance WF, Cochrane MA, Bergen S, Fearnside PM, Delamonica P, Barber C, D'Angelo S, Fernandes T (2001) Environment – the future of the Brazilian Amazon. Science 291:438–439

Laurance WF, Williamson GB (2001) Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. Conserv Biol 15:1529–1535

Laurance WF, Nascimento HEM, Laurance SG, Condit R, D'Angelo S, Andrade A (2004) Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. Forest Ecol Manag 190:131–143

Le Cointe P (1922) L'Amazonie brésilienne. Augustin Challamel (ed.) Librairie Maritime et Coloniale, Paris

Leck MA (1989) Wetland seed banks. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press, London, pp 283–305

Lehmann J, Kaiser K, Peter I (2001) Resin cores for the estimation of nutrient fluxes in highly permeable tropical soil. J Plant Nutri Soil Sci 164:57–64

Lehner B, Döll P (2004) Development and validation of a global database of lakes, reservoirs and wetlands. J Hydrol 296:1–22

Lemes MR, Gribel R, Proctor J, Grattapaglia D (2003) Population genetic structure of mahogany (*Swietenia macrophylla* King, Meliaceae) across the Brazilian Amazon, based on variation at microsatellite loci: implications for conservation. Molecul Ecol 12:2875–2883

Leopold AC (1951) Photoperiodism in plants. Quarterly Rev Biol 26:247–263

Lesack LFW, Melack JM (1991) The deposition, composition, and potential sources of major ionic solutes in rain of the Central Amazon Basin. Water Resources Res 27:2953–2977

Leung AY (1980) Encyclopedia of common natural ingredients used in food, drugs, and cosmetics. Wiley, New York

Levy PE, Meir P, Allen SJ, Jarvis PG (1999) The effect of aqueous transport of CO_2 in xylem sap on gas exchange in woody plants. Tree Physiol 19:53–58

Li M, Lieberman M, Lieberman D (1996) Seedling demography in undisturbed tropical wet forest in Costa Rica. In: Swaine MD (ed) The ecology of tropical forest tree seedlings. MAB UNESCO Series Vol. 17. Parthenon, Paris, pp 285–314

Lieberman M, Lieberman D (1985) Simulation of growth curves from periodic increment data. Ecology 66:632–635

Lieberman D, Lieberman M, Hartshorn G, Peralta R (1985) Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. J Trop Ecol 1:97–109

Lima D (2005) Diversidade socioambiental nas várzeas dos rios Amazonas e Solimões. ProVárzea/IBAMA, Brasilia, Brasil

Lima DM (1999) Equity, sustainable development and biodiversity conservation: Some questions on the ecological partnership in the Amazon. In: Padoch C, Ayres JM, Pinedo-Vasquez M, Henderson A (eds) Várzea: diversity, development, and conservation of Amazonia's whitewater floodplains. The New York Botanical Garden Press, New York, pp 245–263

Lima DM, Alencar E (2000) Histórico da ocupação humana e mobilidade geográfica de assentamentos da várzea do médio Solimões. In: Torres HE, Monteiro H (eds) Populações e meio ambiente. Brasília: Senac and Associação Brasileira De Estudos Populacionais (ABEP), pp 133–161

Lima JR, dos Santos J, Higuchi N (2005) Situação das indústrias madeireiras do estado do Amazonas em 2000. Acta Amazonica 35(2):125–132

de Lima R, Saragoussi M (2000) Floodplain home gardens on the Central Amazon in Brazil. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers bV, Leiden, The Netherlands, pp 243–268

Lima SRM, Veiga VF Jr, Christo HB, Pinto AC, Fernandes PD (2003) In vivo and in vitro studies on anticancer activity of *Copaifera multijuga* Hayne and its fractions. Phytother Res 17:1048–1053

Lima-Ayres D (1992) The social category caboclo: history, social organization, identity and outsider's local social classification of the rural population of an Amazonian region. Ph.D. thesis, University of Cambridge

Lindorf H (1993) Blattstruktur von Pflanzen aus einem feuchten Tropenwald in Venezuela. Bot Jahrb Syst 115(1):45–61

Lipper L (2000) Forest degradation and food security. Unasilva (Forests, food security, and sustainable livelihoods), p 202

Lobo JA, Quesada M, Stoner KE, Fuchs EJ, Herrerias-Diego Y, Rojas J, Saborio G (2003) Factors affecting phenological patterns of bombacaceous trees in seasonal forests in Costa Rica and Mexico. Am J Bot 90:1054–1063

Lobo PC, Joly CA (1998) Tolerance to hypoxia and anoxia in Neotropical tree species. Oecologia Brasiliensis 4:137–156

Lodge DM (1991) Herbivory on freshwater macrophytes. Aquat Bot 41:195–224

Loehle C (1988) Tree life history strategies: the role of defenses. Can J Forest Res 18:209–222

Long SP, Humphries S, Falkowski PG (1994) Photoinhibition of photosynthesis in nature. Annu Rev Plant Physiol Plant Mol Biol 45:633–662

Long SP, Ainsworth EA, Leakey ADB, Nosberger J, Ort D (2006) Food for thought: lower-than-expected crop yield simulation with rising CO2 concentrations. Science 312:1918–1921

Lopes NP, Kato MJ, Andrade EH, Maia JG, Yoshida M, Planchart AR, Katzin AM (1999) Antimalarial use of volatile oil from leaves of *Virola surinamensis* (Rol.) Warb. by Waiapi Amazon Indians. J Ethnopharmacol 67(3):313–319

Lopez A, Hudson JB, Towers GHN (2001) Antiviral and antimicrobial activities of Colombian medicinal plants. J Ethnopharmacol 77(2–3):189–196

Lopez OR (2001) Seed flotation and postflooding germination in tropical terra firme and seasonally flooded forest species. Funct Ecol 15(6):763–771

Lopez OR, Kursar TA (1999) Flood tolerance of four tropical tree species. Tree Physiol 19:925–932

Lopez OR, Kursar TA (2003) Does flood tolerance explain tree species distribution in tropical seasonally flooded habitats? Oecologia 136:193–204

Loustau D, Berbigier P, Roumagnac P, Arruda-Pacheco C, David JS, Ferreira MI, Pereira JS, Tavares R (1996) Transpiration of a 64-year-old maritime pine stand in Portugal. 1. Seasonal course of water flux through maritime pine. Oecologia 107:33–42

Loveland TR, Reed BC, Brown JF, Ohlen DO, Zhu Z, Yang L, Merchant JW (2000) Development of a global land cover characteristics database and IGBP DISCover from 1 km AVHRR data. Int J Remote Sens 21:1301–1330

Loveless MD (1992) Isozyme variation in tropical trees: patterns of genetic organization. New Forests 5:1–28

Lu P, Biron P, Breda N, Granier A (1995) Water relations of adult Norway spruce (*Picea abies* (L) Karst) under soil Drought in the Vosges mountains: water potential, stomatal conductance and transpiration. Ann Sci For 52:117–129

Lucas CM (2008) Within flood season variation in fruit consumption and seed dispersal by two Characin fishes of the Amazon. Biotropica 40(5):581–589

Lugo AE (1992) Comparison of tropical tree plantations with secondary forests of similar age. Ecol Monogr 62(1):1–41

Luizão FJ (1989) Litter production and mineral element input to the forest floor in a central Amazonian forest. GeoJournal 19:407–417

Luna FMS (2004) Ethnobotany of the communities of the upper Rio Nangaritza. Lyonia 7(2): 105–122

Lundberg JG, Marshall LG, Guerrero J, Horton B, Malabarba MCSL, Wesselingh F (1998) The stage for neotropical fish diversification. In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CAS (eds) Phylogeny and classification of Neotropical fishes. EDIPUCRS, Porto Alegre, pp 13–48

Maas PJM, Vestra LY (1993) Neotropical plant families. Koeltz Scientific Books, Königstein

Mabberley DJ (1997) The plant book, 2nd edn. Cambridge University Press, Cambridge, p 857

Macedo DS, Anderson AB (1993) Early ecological changes associated with logging in an Amazon floodplain. Biotropica 25(2):151–163

Macedo M, Prance GT (1978) Notes on the vegetation of Amazonia II. The dispersal of plants in Amazonian white sand campinas: the campinas as functional islands. Brittonia 30:203–215

Machado JL, Tyree MT (1994) Patterns of hydraulic architecture and water relations of two tropical canopy trees with contrasting leaf phenologies: *Ochroma pyramidale* and *Pseudobombax septenatum*. Tree Physiol 14:219–240

Mack AL (1998) An advantage of large seed size: tolerating rather than succumbing to seed predators. Biotropica 30:604–608

Magalhães FMM (1986) O estado atual do conhecimento sobre fixação biológica de nitrogênio na Amazônia. In: Emprapa-CPATU, Anais vol 1. Clima e solo, Belem 1986. Simpósio do Trópico Umido, Belem, 1984, pp 499–512

Magurran AE (1988) Ecological diversity and its measurement. Chapman & Hall, London, p 179

Maia LA (1997) Influência do pulso de inundação na fisiologia, fenologia e produçao de frutos de *Hevea spruceana* (Euphorbiaceae) e *Eschweilera tenuifolia* (Lecythidaceae), em área inundável de igapó da Amazônia central. Unpublished Ph.D. Thesis, INPA/FUA Manaus, p 186

Maia LA (2001) Frutos da Amazônia: fonte de alimento para peixes. INPA Manaus: Serviço de Apoio às Micro e Pequenas Empresas do Amazonas/Sebrae, p 143

Maia LA, Chalco FP (2002) Produçao de frutos de espécies da floresta de várzea da Amazônia central importantes na alimentaçao de peixes. Acta Amazonica 32:45–54

Maia LA, Maia S, Parolin P (2005) Seedling morphology of tree species in central Amazonian várzea floodplain forests. Ecotropica 11:1–8

Maia LA, Santos LM, Parolin P (2007) Seed germination of *Bothriospora corymbosa* (Rubiaceae) recuperated from the digestive tract of *Triportheus angulatus* (sardine) in Camaleão Lake, Central Amazonia. Acta Amazonica 37:321–326

Malhi Y, Nobre AD, Grace J, Kruijt B, Pereira MGP, Culf A, Scott S (1998) Carbon dioxide transfer over a central Amazonian rain forest. J Geophys Res 103(D24):31593–31612

Malhi Y, Grace J (2000) Tropical forests and atmospheric carbon dioxide. Trees 15:332–337

Malhi Y, Baker TR, Phillips OL, Almeida S, Alvarez E, Arroyo L, Chave J, Czimczik CI, Di Fiore A, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis LL, Montoya LMM, Monteagudo A, Neill DA, Núñez Vargas P, Patiño S, Pitman NCA, Quesada CA, Salomão R, Silva JNM, Lezama AT, Martínez RV, Terborgh J, Vinceti B, Lloyd J (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. Global Change Biol 10:563–591

Malhi Y, Wood D, Baker TR, Wright J, Phillips OL, Cochrane T, Meir P, Chave J, Almeida S, Arroyo L, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Monteagudo A, Neill DA, Núñez Vargas P, Pitman NCA, Quesad CA, Salomão R, Silva JNM, Lezama AT, Terborgh J, Martínez RV, Vinceti B (2006) The regional variation o aboveground live biomass in old-growth Amazonian forests. Global Change Biol 12:1107–1138

Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li W, Nobre CA (2008) Climate change, deorestation, and fate of the Amazon. Science 319:169–172

Malloch DW, Pirozynski KA, Raven PH (1980) Ecological and evolutionary significance of mycorrhizal symbiosis in vascular plants (a review). Proc Nat Acad Sci USA 77:2113–2118

Mannheimer S, Bevilacqua G, Caramaschi EP, Scarano FR (2003) Evidence for seed dispersal by the catfish *Auchenipterichthys longimanus* in an Amazonian lake. J Trop Ecol 19:215–218

Mano Y, Omori F, Takamizo T, Kindiger B, McK BR, Loaisiga CH (2006) Variation for root aerenchyma formation in flooded and non-flooded maize and teosinte seedlings. Plant Soil 281:269–279

Marengo JA (1992) Interannual variability of surface climate in the Amazon basin. J Climatol 12:853–863

Marengo JA (2006) Mudancas climáticas globais e seus efeitos sobre a biodiversidade. Caracterizacao do clima atual e definicao das alteracoes climaticas para o territorio Brasileiro ao longo do seculo XXI. Biodiversidade 26, Brasilia DF, pp 1–163

Marengo JA, Tomasella J, Uvo CR (1998) Trends in streamflow and rainfall in tropical South America: Amazonia, eastern Brazil and north-western Peru. J Geophys Res 103(D2):1775–1783

Marengo JA, Nobre CA, Tomasella J, Cardoso MF, Oyama MD (2008) Hydro-climatic and ecological behaviour of the drought of Amazonia in 2005. Philos T Roy Soc B 363:1773–1778

Mariaux A (1967) Les cernes dans les bois tropicaux africains, nature e périodicité. Bois et Fôrets des Tropiques 113:3–14

Marinho TAS (2008) Distribuição e estrutura da população de quatro espécies madeireiras em uma floresta sazonalmente alagável na Reserva de Desenvolvimento Sustentável Mamirauá, Amazônia Central. Master-Diss. Instituto Nacional de Pesquisas da Amazônia, Manaus

Marques CA (2001) Importância econômica da família Lauraceae Lindl. Floresta e Ambiente 8(1):195–206

Marques MCM (1994) Estudos auto-ecológicos do guanandi (*Calophyllum brasiliense* Camb. Clusiaceae) em mata ciliar no município de Brotas, SP. Unpublished M.Sc. Thesis, Campinas

Marquis RJ (1988) Phenological variation in the neotropical understory shrub Piper arieianum: causes and consequences. Ecology 69:1552–1565

Martinelli LA, Victoria RL, Trivelin PCO, Devol AH, Richey JE (1992) ^{15}N Natural abundance in plants of the Amazon River floodplain and potential atmospheric N_2 fixation. Oecologia 90:591–596

Martinelli LA, Piccolo MC, Townsend AR, Vitousek PM, Cuevas E, Mcdowell W, Robertson GP, Santos OC, Treseder K (1999) Nitrogen stable isotopic composition of leaves and soil: tropical versus temperate forests. Biogeochemistry 46:45–65

Martinelli LA, Almeida S, Brown IF, Moreira MZ, Victoria RL, Filoso S, Ferreira CAC, Thomas WW (2000) Variation in nutrient distribution and potential nutrient losses by selective logging in a humid tropical forest of Rondônia, Brazil. Biotropica 31:597–613

Martinez J-M, Le Toan T (2007) Mapping of flood dynamics and spatial distribution of vegetation in the Amazon floodplain using multitemporal SAR data. Remote Sens Environ 108:209–223

Martini A, Araújo Rosa N, Uhl C (1998) Espécies de árvores potencialmente ameaçadas pela atividade madeireira na Amazônia. Imazon, Belém, Brazil, Série Amazônia N° 11

Martins AP, Salgueiro LR, Da Cunha AP, Vila R, Canigueral S, Tomi F, Casanova J (Nov/Dec 2003) Chemical composition of the bark oil of *Cedrela odorata* from S. Tomé & Principe. J Essential oil Res (15)6

Martius C (1989) Untersuchungen zur Ökologie des Holzabbaus durch Termiten (Isoptera) in zentralamazonischen Überschwemmungswäldern. Afra, Frankfurt

Martius C (1992) Density, humidity, and nitrogen content of dominant wood species of floodplain forests (várzea) in Amazonia. Holz Roh Werkst 50:300–303

Martius C (1997) The termites. In: Junk WJ (ed) The Central Amazon floodplain: ecology of a pulsing system. Ecol Stud 126:362–371. Springer, Berlin/Heidelberg/New York

Maslin MA, Burns SJ (2000) Reconstruction of the Amazon basin effective moisture availability over the past 14, 000 years. Science 290:2285–2287

Matson PA, McDowell WH, Townsend AR, Vitousek PM (1999) The globalization of N deposition: ecosystem consequences in tropical environments. Biogeochemistry 46:67–83

Maurenza D (2007) Respostas ecofisiológicas ao estresse por inundação em duas espécies de plântulas da várzea, Amazônia Central. Master-Diss. Instituto Nacional de Pesquisas da Amazônia, Manaus

May DJ, Killingbeck KT (1992) Effects of preventing nutrient resorption on plant fitness and foliar nutrient dynamics. Ecology 73:1868–1878

Mayhew JE, Newton AC (1998) The silviculture of Mahagony. CABI Publishing, London

Mayle FE, Burbridge R, Killeen TJ (2000) Millennial-scale dynamics of southern Amazonian rain forests. Science 290:2291–2294

Mayorga E, Logsdon MG, Ballester MVR, Richey JE (2005) Estimating cell-to-cell surface drainage paths from digital networks, with an application to the Amazon basin. J Hydrol 315:167–182

McCormick JF (1979) A summary of the national riparian symposium. In: U.S. department of agriculture, forest service (ed) Strategies for protection and management of floodplain wetlands and other riparian ecosystems, Ge Tech Rep WO-12 US. Department of Agriculture, Forest Service, Washington DC, pp 362–363

McDonald MP, Galwey NW, Colmer TD (2002) Similarity and diversity in adventitious root anatomy as related to root aeration among a range of wetland and dryland grass species. Plant Cell Environ 25:441–451

McGrath DG, Castro F, Futemma CR (1994) Reservas de lago e o manejo comunitário da pesca no Baixo Amazonas: Uma avaliação preliminar. In: D'Incao MA, Silveira IM (eds) Amazônia e a crise da modernização. Museu Paraense Emílio Goeldi, Belém, Pará, pp 389–402

McGrath D, de Castro F, Câmara E, Futemma C (1999) Community management of floodplain lakes and the sustainable development of Amazonian fisheries. In: Padoch C, Ayres JM, Pinedo-Vasquez M, Henderson A (eds) Várzea – diversity, development, and conservation of Amazonia's Whitewater floodplains. Advances in economic botany, vol 13. The New York Botanical Garden Press, New York, pp 59–82

McGrath DG, da Gama ASP (2005) A situação fundiária da várzea do Rio Amazonas e experimentos de regularização fundiária nos estados do pará e do Amazonas. In: Benfatti JH, Surgik ACS, Treccani GD, McGrath DG, da Gama ASP (eds) Aquestão fundiária e o maejo dos recursos naturais da várzea: análise para a elaboração de novos modelos jurídicos. ProVárzea/IBAMA, Manaus, Brazil, pp 35–52

Meave J, Kellman M (1994) Maintenance of rain forest diversity in riparian forests of tropical savannas: implications for species conservation during Pleistocene drought. J Biogeogr 21:121–135

Meave J, Kellman M, MacDougall A, Rosales J (1991) Riparian habitats as tropical forest refugia. Global Ecol Biogeogr Lett 1:69–76

Medina E (1983) Adaptations of tropical trees to moisture stress. In: Golley FB (ed) Ecosystems of the world: tropical rain forest ecosystems. Elsevier Scientific Publishing Company, Amsterdam/Oxford/New York, pp 225–237

Medina E (1984) Nutrient balance and physiological processes at the leaf level. In: Medina E, Mooney HA, Vazques-Yanes C (eds) Physiological ecology of plants of the wet tropics. Junk Publ Kluwer, Boston, pp 134–154

Medina E, Lieth H (1964) Die Beziehungen zwischen Chlorophyllgehalt, assimilierender Fläche und Trockensubstanzproduktion in einigen Pflanzengemeinschaften. Beitr Biol Pflanzen 40:451–494

Medina E, Klinge H (1983) Productivity of tropical forests and tropical woodlands. Encyclopedia Plant Physiol 12D:281–303. Springer, Berlin, Heidelberg

Medina E, Garcia V, Cuevas E (1990) Sclerophylly and oligotrophic environment. Relationships between leaf structure, mineral nutrient content and drought resistance in tropical rain forest of the upper Rio Negro regions. Biotropica 22:51–64

Medri ME, Ferreira ACS, Kolb RM, Bianchini E, Pimenta JA, Davanso-Fabro VM, Medri C (2007) Alterações morfoanatômicas em plantas de Lithraea molleoides (Vell.) Engl. submetidas ao alagamento. Acta Scientiarum (29):15–22

Meggers BJ (1984) The indigenous peoples of Amazonia, their cultures, land use patterns and effect on the landscape and biota. In: Sioli H (ed) The Amazon – Limnology and landscape ecology of a mighty tropical river and its basin. Monographie Biologicae, Junk, Dordrecht, pp 627–648

Megonigal JP, Vann CD, Wolf AA (2005) Flooding constraints on tree (*Taxodium distichum*) and herb growth responses to elevated CO_2. Wetlands 25:430–438

Meinzer FC (2005) Regulation of water flux through tropical forest canopy trees: do universal rules apply? Tree Physiol 21:19–26

Meinzer FC, Goldstein G, Franco AC, Bustamante M, Igler E, Jackson P, Caldas L, Rundel PW (1999) Atmospheric and hydraulic limitations on transpiration in Brazilian Cerrado woody species. Funct Ecol 13:273–282

Meir P (1996) The exchange of carbon dioxide in tropical forests. Ph.D. thesis, University of Edinburgh

Melack JM (2004) Remote sensing of tropical wetlands. In: Ustin S (ed) Manual of remote sensing, vol 4. Remote Sensing for natural resources management and environmental monitoring. Wiley, New York, pp 319–343

Melack JM, Fisher TR (1988) Denitrification and nitrogen fixation in an Amazon floodplain lake. Verh Internat Verein Limnol 23:2232–2236

Melack JM, Hess LL (2004) Remote sensing of wetlands on a global scale. SIL News 42:1–5

Melack JM, Hess LL (2010) Remote sensing of the distribution and extent of wetlands in the Amazon basin. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Melack JM, Hess LL, Sippel S (1994) Remote sensing of lakes and floodplains in the Amazon basin. Remote Sens Rev 10:127–142

Melack JM, Hess LL, Gastil M, Forsberg BR, Hamilton SK, Lima IBT, Novo EMLM (2004) Regionalization of methane emissions in the Amazon Basin with microwave remote sensing. Global Change Biol 10(5):530–544

Melillo JM, McGuire AD, Kicklighter DW, Moore B III, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. Nature 363:234–240

Melo FPL, Neto AVA, Simabukuro EA, Tabarelli M (2004) Recrutamento e Estabelecimento de Plântulas. In: Ferreira AG, Borghetti F (eds) Germinação: do básico ao aplicado, pp 237–250

Menezes Neto MA (1994) Influência da disponibilidade de oxigênio sobre a germinação, crescimento, e atividade das enzimas álcooldesidrogenase e lactato desidrogenase em Açaí (Euterpe oleracea Mart.). Dissertação de Mestrado, Escola Superior de Agricultura de Lavras, Minas Gerais, Brasil, p 50

Menton MC (2003) Effects of logging on non-timber forest product extraction in the Brazilian Amazon: community perceptions of change. Int Forest Rev 5(2):97–105

Mertes LAK (1994) Rates of flood-plain sedimentation on the central Amazon River. Geology 22:171–174

Mertes LAK, Smith MO, Adams JB (1993) Estimating suspended sediment concentrations in surface waters of the Amazon River wetlands from Landsat images. Remote Sens Environ 42:281–301

Mertes LAK, Daniel DL, Melack JM, Nelson B, Martinelli A, Forsberg BR (1995) Spatial patterns of hydrology, geomorphology, and vegetation on the floodplain of the Amazon River in Brazil from a remote sensing perspective. Geomorphology 13:215–232

Mesquita RCG (2000) Management of advanced regeneration in secondary forests of the Brazilian Amazon. Forest Ecol Manag 130:131–140

Metcalfe CR, Chalk L (1950) Anatomy of the dicotyledones, vol I. Nr II Clarendon, Oxford

Metcalfe DJ, Grubb PJ (1995) Seed mass and light requirements for regeneration in Southeast Asian rainforest. Can J Bot 73:817–826

Metzger JP, Bernacci LC, Goldenberg R (1997) Pattern of tree species diversity in riparian forest fragments of different widths. Plant Ecol 133:135–152

Meyer FH (1967) Feinwurzelverteilung bei Waldbäumen in Abhängigkeit vom Substrat. Forstarchiv 38:286–290

Meyer U (1991) Feinwurzelsysteme und Mykorrhizatypen als Anpassungsmechanismen in zentralamazonischen Überschwemmungswäldern- Igapó and Várzea. Ph.D. thesis, University of Hohenheim, Germany

Meyer U, Junk WJ, Linck C (2010) Fine root systems and mycorrhizal associations in two central Amazonian floodplain forests – igapó and várzea. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Middleton B (2000) Hydrochory, seed banks, and regeneration dynamics along the landscape boundaries of a forested wetland. Plant Ecol 146:169–184

Millard P, Proe MF (1991) Leaf demography and the seasonal internal cycling of nitrogen in sycamore (*Acer pseudoplatanus* L) seedlings in relation to nitrogen supply. New Phytolt 117:587–596

Miquel S (1987) Morphologie fontionelle de plantules d'espèces forestières Humides d'Afrique. Rapport du Séminaire sous-régional, 1-8 juillet 1985, Makokou, Gabon. UNESCO, Paris

Mitaine-Offer AC, Sauvain M, Petermann C, Zeches-Hanrot M (2001) Constituents of the trunk bark of *Maquira coriacea*. Fitoterapia 72(7):841–843

Mitsch WJ, Gosselink JG (2000) Wetlands. Wiley, New York

Moegenburg SM (1996) *Sabal palmetto* seed size: causes of variation, choices of predators, and consequences for seedlings. Oecologia 106:539–543

Moegenburg SM (2002) Spatial and temporal variation in hydrochory in Amazonian floodplain forest. Biotropica 34:606–612

Moegenburg SM, Levey DJ (2003) Do frugivores respond to fruit harvest? An experimental study of short-term responses. Ecology 84:2600–2612

Moles AT, Westoby M (2006) Seed size and plant strategy across the whole life cycle. Oikos 113:91–105

Mommer L, Visser EJW (2005) Underwater photosynthesis in flooded terrestrial plants: a matter of leaf plasticity. Annal Bot 96:581–589

Mommer L, Lenssen JPM, Huber H, Visser EJW, De Kroon H (2006) Ecophysiological determinants of plant performance under flooding: a comparative study of seven plant families. J Ecol 94:1117–1129

Mooney HA, Björkman O, Hall AE, Medina E, Tomlinson PB (1980) The study of the physiological ecology of tropical plants – current status and needs. BioScience 30:22–26

Moreau S, Le Toan T (2003) Biomass quantification of Andean wetland forages using ERS satellite SAR data for optimizing livestock management. Remote Sens Environ 84:477–492

Moreira E (1970) Os Igapós e seu aproveitaniento. Imprensa Universitaria, Belém – Pará

de Moreira FMS, da Silva MF, de Faria SM (1992) Occurrence of nodulation in legume species in the Amazon region of Brazil. New Phytol 121:563–570

de Moreira FMS, Gillis M, Pot B, Kersters K, Franco AA (1993) Characterisation of rhizobia isolated from different divergence groups of tropical Leguminosae by Comparative Polyacrylamide Gel Electrophoresis of their total proteins. System Appl Microb 16:135–146 de Moreira FMS, Haukka K, Young JPW (1998) Biodiversity of rhizobia isolated from a wide range of forest legumes in Brazil. Molecul Ecol 7(7):889–895

Moreira KS (2006) Avaliação da sazonalidade sobre a dinâmica de liteira em uma floresta de transição no Parque Estadual do Cantão, entorno da Ilha do Bananal, estado do Tocantins. Universidade Federal do Tocantins

Moretti C, Bhatnagar S, Beloeil JC, Polonsky J (1986) Two new quassinoids from *Simaba multiflora* fruits. J Nat Prod 49(3):440–444

Mori SA, Brown JL (1994) Report on wind dispersal in a lowland moist forest in Central French Guiana. http://www.nybg.org/bsci/french_guiana/wind.html

Motzer T, Munz N, Küppers M, Schmitt D, Anhuf D (2005) Stomatal conductance, transpiration and sap flow of tropical montane rain forest trees in the southern Ecuadorian Andes. Tree Physiol 25:1283–1293

Moyersoen B, Becker P, Alexander IJ (2001) Are ectomycorrhizas more abundant than arbuscular mycorrhizas in tropical heath forests? New Phytol 150:591–599

Müller D, Nielson J (1965) Production brute, pertes par respiration et production nette dans la foret ombrophile tropicale. Forstl Forsogsvaes Dan 29:69–160

Müller E (2002) Water relations and stem water usage of trees from the Central Amazonian white-water floodplain (Várzea). Lieberei R, Bianchi H-K, Boehm V, Reissdorff C (eds) Proceedings of the German-Brazilian workshop Hamburg 2000. GKSS Geesthacht, pp 623–627

Müller J, Irion G, Nunes De Mello J, Junk WJ (1995) Hydrological changes of the Amazon during the last glacial-interglacial cycle in Central-Amazonia (Brazil). Naturwissenschaften 82:232–235

Murali K, Sukumar SR (1994) Reproductive phenology of a tropical dry forest in Mudumalai, southern India. J Ecol 82:759–767

Murray K, Feinsinger GP, Busby HW, Linhart YB, Beach JH, Kinsman S (1987) Evaluation of character displacement among plants in two tropical pollination guilds. Ecology 68:1283–1293

Nadelhoffer KJ, Aber JD, Melillo JM (1985) Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Ecology 66(4):1377–1390

Napp-Zinn K (1973) Anatomie des Blattes II; Blattanatomie der Angionspermen, Entwicklungsgeschichtliche und topographische Anatomie des Angiospermenblattes. Gebrueder Borntraeger, Berlin, Stuttgart

Nassif SML, Israel GV, Fernandes GD (1998) Fatores externos (ambientais) que influenciam na germinação de sementes. Informativo Sementes IPEF – Abril 1998

Navarro G, Maldonado M (2002) Geografía Ecológica de Bolivia: Vegetación y Ambientes Acuáticos. Centro de Ecología Simón I, Patiño/Santa Cruz/Bolivia

Nebel G (2001) *Minquartia guianensis* Aubl.: use, ecology and management in forestry and agroforestry. Forest Ecol Manag 150:115–124

Nebel G, Dragsted J, Salazar Vega A (2001a) Litter fall, biomass and net primary production in flood plain forests in the Peruvian Amazon. Forest Ecol Manag 150:93–102

Nebel G, Dragsted J, Simonsen TR, Vanclay JK (2001b) The Amazon flood plain forest tree *Maquira coriacea* (Karsten) CC Berg: aspects of ecology and management. Forest Ecol Manage 150:103–113

Nebel G, Dragsted J, Vanclay JK (2001c) Structure and floristic composition of floodplain forests in the Peruvian Amazon: II. The understorey of restinga forests. Forest Ecol Manag 150:59–77

Nebel G, Kvist LP, Vanclay JK, Christensen H, Freitas L, Ruíz J (2001d) Structure and floristic composition of floodplain forests in the Peruvian Amazon: I. Overstorey. Forest Ecol Manag 150:27–57

Nebel G, Kvist LP, Vanclay JK, Vidaurre H (2001e) Forest dynamic in flood plain forests in the Peruvian Amazon: effects of disturbance and implications for management. Forest Ecol Manag 150:79–92

Nebel G, Meilby H (2005) Growth and population structure of timber species in Peruvian flood plains. Forest Ecol Manag 215:196–211

Neeff T, Santos JR (2005) A growth model for secondary forest in Central Amazonia. Forest Ecol Manag 216:270–282

Neff JC, Holland EA, Dentener FJ, McDowell WH, Russell KM (2002) The origin, composition and rates of organic nitrogen deposition: a missing piece of the nitrogen cycle? Biogeochemistry 57:99–136

Negisi K (1979) Bark respiration rate in stem segments detached from young *Pinus densiflora* trees in relation to velocity of artificial sap flow. J Jap For Soc 61:88–93

Neill C, Piccolo MC, Melillo JM, Steudler PA, Cerri CC (1999) Nitrogen dynamics in Amazon forest and pasture soils measured by ^{15}N pool dilution. Soil Biol Biochem 31:567–572

Nepstad DC, Carvalho CR, Davidson EA, Jipp PH, Lefebvre PA, Negreiros GH, Silva ED, Stone TA, Trumbore SE, Vieira S (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372:666–669

Nepstad DC, Veríssimo A, Alencar A, Nobre CA, Lima E, Lefebvre P, Schlesinger P, Potter C, Moutinho P, Mendoza E, Cochrane M, Brooks V (1999) Large-scale impoverishment of Amazonian forests by logging and fire. Nature 398:505–508

Nepstad DC, Carvalho G, Barros AC, Alencar A, Capobianco JP, Bishop J, Moutinho P, Lefebvre P, Silva UL Jr, Prins E (2001) Road paving, fire regime feedbacks, and the future of Amazon forests. Forest Ecol Manage 154:395–407

Nepstad DC, Stickler CM, Soares-Filho BS, Merry F (2008) Interactions among Amazon land use, forests and climate: prospects for a near-term forest tipping point. Philos T Roy Soc B 363:1737–1746

Newsome RD, Kozlowski TT, Tang ZC (1982) Responses of *Ulmus americana* seedlings to flooding of soil. Can J Bot 60:1688–1695

Ng FSP (1978) Strategies of establishment in Malayan forest trees. In: Tomlinson PB, Zimmerman M (eds) Tropical trees as living systems. Cambridge University Press. New York, pp 129–162

Nielsen HB, Hazell A, Hazell R, Ghia F, Torrsell KBG (1994) Indole alkaloids and terpenoids from *Tabernaemontana markgrafiana*. Phytochemistry 37(6):1729–1735

Nilsen EKT, Orcutt DM (1996) Physiology of plants under stress: abiotic actors. Wiley, New York

Niner BM, Hirsch AM (1998) How many *Rhizobium* genes, in addition to nod, nif/fix, and exo, are needed for nodule development and function? Symbiosis 24:51–102

Noda SN, Noda H, dos Santos HP (2000) Family farming systems in the floodplains of the state of Amazonas. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers bV, Leiden, The Netherlands, pp 215–242

Non-timber forest products – NTFP (2007) NTFP webpage http//www.ntfp.org/definition.html. Accessed 12 March 2007

Norris DO (1965) Acid production by *Rhizobium* a unifying concept. Plant Soil 22(2):143–166

Norris DO (1969) Observation on the nodulation status of rainforest leguminous species in Amazonia and Guyana. Trop Agric 46:145–151

Nouchi I, Mariko S, Aoki K (1990) Mechanism of methane transport from the rhizosphere to the atmosphere through rice plants. Plant Physiol 94:59–66

Novick RS, Dick CW, Lemes M, Navarro C, Caccone A, Bermingham E (2003) Genetic structure of Mesoamerican populations of big-leaf mahogany (*Swietenia macrophylla*) inferred by microsatellite analysis. Molecul Ecol 12:2885–2893

Novo EMLM, Shimabukuro YE (1997) Identification and mapping of the Amazon habitats using a mixing model. Int J Remote Sens 18:663–670

Novo EMLM, Leite FA, Avila J, Ballester V, Melack JM (1997) Assessment of Amazon floodplain habitats using TM/Landsat data. Ciencia e Cultura 49:280–284

Nunes da Cunha C, Junk WJ (1999) Composição florística de capões e cordilheiras: localização das espécies lenhosas quanto ao gradiente de inundação no Pantanal de Poconé, MT – Brasil. In: EMBRAPA (ed) Anais do II Simpósio sobre Recursos Naturais e Sócio-economicos do Pantanal. Manejo e Conservação. EMBRAPA, Corumbá, pp 17–28

Nunes da Cunha C, Junk WJ (in press) A preliminary classification of habitats of the Pantanal of Mato Grosso and Mato Grosso do Sul, and its relation to international wetland classification systems. Pensoft, Sofia-Moskow

Nuñez-Iturri G, Howe HF (2007) Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain Forest in western Amazonia. Biotropica 39:316–327

Oberbauer FS, Strain BR (1984) Photosynthesis and successional status of Costa Rican rain forest trees. Photosynth Res 5:227–232

Odum EP (1981) Foreword. In: Clark JR, Benforado J (eds) Wetlands of bottomland hardwood forests. Elsevier, Amsterdam, pp 8–10

Oga S, Sertie SA, Brasile AC, Hanada S (1981) Anti-inflammatory effect of crude extract from *Guarea guidonia*. Planta Med 42(3):310–312

Ohly JJ (2000a) Artificial pastures on Central Amazonian floodplains. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers bV, Leiden, The Netherlands, pp 291–311

Ohly JJ (2000b) Development of Central Amazonia in the modern era. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers bV, Leiden, pp 27–73

Ohly JJ, Hund M (2000) Floodplain animal husbandry in Central Amazonia. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers bV, Leiden, The Netherlands, pp 313–343

Oliveira AA, Mori SA (1999) A central Amazonian terra firme forest. I. High tree species richness on poor soils. Biodiversity and conservation 8:1219–1244

Oliveira AA, Nelson BW (2001) Floristic relationships of terra firme forests in the Brazilian Amazon. Forest Ecol Manag 146:169–179

Oliveira AC (1998) Aspectos da dinâmica populacional de *Salix martiana* Leyb (Salicaceae), em áreas de várzea da Amazônia Central. Master Thesis INPA/FUA, pp 83

Oliveira AC, Piedade MTF (2002) Implicações ecológicas da fenologia reprodutiva de *Salix martiana* Leyb. (Salicaceae) em áreas de várzea da Amazônia Central. Acta Amazonica 32:377–385

de Oliveira LA, Moreira FW, Falcão NP, Pinto VSG (2000) Floodplain soils of central Amazonia: chemical and physical characteristics and agricultural sustainability. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers bV, Leiden, The Netherlands, pp 129–140

Oliveira PHF, Artaxo P, Pires C, De Lucca S, Procópio A, Holben B, Schafer J, Cardoso LF, Wofsy SC, Rocha HR (2007) Effects of biomass burning aerosols and clouds on the CO_2 flux in Amazonia. Tellus B 59:338–349

Oliveira Wittmann A (2007) Conteúdo de tocromanóis em espécies arbóreas de várzea da Amazônia Central sob condições controladas. Tese INPA/UFAM, p 126

Oliveira Wittmann A de, Lopes A, Conserva A dos S, Piedade MTF (2010) Germination and seedling establishment in floodplain forests. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Oliveira Wittmann A, Piedade MTF, Wittmann F, Parolin P (2007) Germination in four low-várzea tree species of Central Amazonia. Aquat Bot 86(3):197–203

Oliveira Wittmann A, Piedade MTF, Wittmann F, Schöngart J, Parolin P (2007) Patterns of structure and seedling diversity along a flooding and successional gradient in Amazonian floodplain forests. Pesqui Botân 58:199–138

Oliveira-Filho AT, Vilela EA, Gavilanes ML, Carvalho DA (1994) Effect of flooding regime and understorey bamboos on the physiognomy and tree species composition of a tropical semi deciduous forest in South-eastern Brazil. Vegetatio 113:99–124

Ometto JPHB, Nobre AD, Rocha HR, Artaxo P, Martinelli LA (2005) Amazônia and the modern carbon cycle: lessons learned. Oecologia 143:483–500

Opler PA, Frankie GW, Baker HG (1976) Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. J Biogeogr 3:231–236

Oren R, Zimmermann R, Terborgh J (1996) Transpiration in upper Amazonia floodplain and upland forests in response to drought-breaking rains. Ecology 77:968–977

Osman AM, Milthorpe FL (1971) Photosynthesis of wheat leaves in relation to age, illuminance and nutrient supply. II Results. Photosynthetica 5:61–70

Overman JPM, Witte HJL, Saldarriaga JG (1994) Evaluation of regression models for above-ground biomass determination in Amazon rain forest. J Trop Ecol 10:207–218

Oyama MD, Nobre CA (2004) A simple potential vegetation model for coupling with the Simple Biosphere Model (SiB). Rev Bras Meteorol 19:203–216

Padoch C (1988) The economic importance of marketing of forest and fallow products in the Iquitos region. Adv Econom Bot 5:74–89

Padoch C, Ayres JM, Pinedo-Vasquez M, Henderson A (1999) Várzea: diversity, development, and conservation of Amazonia's whitewater floodplains. The New York Botanical Garden Press, New York

Padovani CR, Forsberg BR, Pimentel TP (1995) Contaminação mercurial em peixes do Rio Madeira: resultados e recomendações. Acta Amazonica 25(5):127–136

Panshin AJ, De Zeeuw C (1980) Textbook of wood technology, 4th edn. MacGraw-Hill, New York

Parker EP (1989) A neglected human resource in Amazonia: the Amazon Caboclo. In: Posey DA, Balee W (eds) Resource management in Amazonia: indigenous and folk strategies. Adv Econom Bot 7:249–259. The New York Botanical Garden, New York

Parolin P (1997) Auswirkungen periodischer Vernässung und Überflutung auf Phänologie, Photosynthese und Blattphysiologie von Baumarten unterschiedlicher Wachstumsstrategie in zentralamazonischen Überschwemmungsgebieten. Unpublished Ph.D. thesis, University of Hamburg, p 156

Parolin P (1998) Floristic composition and structure of two stands of *Senna reticulata* differing in age. Amazoniana 15(1/2):113–128

Parolin P (2000a) Growth, productivity, and use of trees in white water floodplains. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers b.V, Leiden, pp 375–391

Parolin P (2000b) Seed mass in Amazonian floodplains forest with contrasting nutrients supplies. J Trop Ecol 16:417–428

Parolin P (2000c) Phenology and CO_2-assimilation of trees in Central Amazonian floodplains. J Trop Ecol 16:465–473

Parolin P (2000d) Physiology of trees in the floodplains of the Amazon. Botanica 50:48–56

Parolin P (2001a) Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. Oecologia 128:326–335

Parolin P (2001b) Phenology and photosynthesis of six tree species in Central Amazonian floodplains. In: Palo M, Uusivuori J, Mery G (eds) World forests, markets and policies. World forests vol III. Kluwer, Dordrecht/London/Boston, pp 304–305

Parolin P (2001c) *Senna reticulata*, a pioneer tree from Amazonian várzea floodplains. Bot Rev 67:239–254

Parolin P (2001d) Seed germination and early establishment in 12 tree species from nutrient-rich and nutrient-poor Central Amazonian floodplains. Aquat Bot 70:89–103

Parolin P (2002a) Life history and environment of *Cecropia latiloba* in Amazonian floodplains. Rev Biol Trop 50:531–545

Parolin P (2002b) Radial gradients in wood specific gravity in trees of central Amazonian floodplains. IAWA J 23(4):449–457

Parolin P (2002c) Seasonal changes of specific leaf mass and leaf size in trees of Amazonian floodplains. Phyton 42:169–185

Parolin P (2002d) Submergence tolerance vs. escape from submergence: two strategies of seedling establishment in Amazonian floodplains. Environm Experim Bot 48(2):177–186

Parolin P (2003) Extreme sites and diversity – an example from Amazonian floodplain forests. Botanica 53:23–34

Parolin P (2009) Submerged in darkness: adaptations to prolonged submergence by woody species of the Amazonian floodplains. Annal Bot Flood Spec Issue 103:359–376

Parolin P, Ferreira LV (1998) Are there differences in specific wood gravities between trees in várzea and igapó (Central Amazonia)? Ecotropica 4:25–32

Parolin P, Ferreira LV, Junk WJ (1998) Central Amazonia floodplains: effect of two water types on the wood density of trees. Verh Internat Verein Limnol 26:1106–1112

Parolin P, Worbes M (2000) Wood density of trees in black water floodplains of Rio Jaú National Park, Amazonia. Acta Amazonica 30(3):441–448

Parolin P, Junk WJ, Piedade MTF (2001) Gas exchange of six tree species from Central Amazonian floodplains. Trop Ecol 42(1):15–24

Parolin P, Junk WJ (2002) The effect of submergence on seed germination in trees from Amazonian floodplains. Bol Mus Par Emilio Goeldi Ser Bot 18:321–329

Parolin P, Armbrüster N, Junk WJ (2002a) Seasonal changes of leaf nitrogen content in trees of Amazonian floodplains. Acta Amazonica 32(2):231–240

Parolin P, Armbrüster N, Wittmann F, Ferreira LV, Piedade MTF, Junk WJ (2002b) A review of tree phenology in central Amazonian floodplains. Pesqui Botân 52:195–222

Parolin P, Oliveira AC, Piedade MTF, Wittmann F, Junk WJ (2002c) Pioneer trees in Amazonian floodplains: key species form monospecific stands in different habitats. Folia Geobotan 37:225–238

Parolin P, Ferreira LV, Junk WJ (2003) Germination characteristics and establishment of trees from Central Amazonian floodplains. Trop Ecol 44:155–167

Parolin P, Adis J, Rodrigues WA, Amaral I, Piedade MTF (2004a) Floristic study of an igapó floodplain forest in Central Amazonia, Brazil (Tarumã-Mirim, Rio Negro). Amazoniana 18(1/2):29–47

Parolin P, De Simone O, Haase K, Waldhoff D, Rottenberger S, Kuhn U, Kesselmeier J, Schmidt W, Piedade MTF, Junk W (2004b) Central Amazon floodplain forests: tree survival in a pulsing system. Botan Rev 70:357–380

Parolin P, Müller E, Junk WJ (2005) Water relations of Amazonian várzea trees. Int J Ecol Environ Sci 31:361–364

Parolin P, Armbrüster N, Junk WJ (2006) Two Amazonian floodplain trees react differently to periodical flooding. J Trop Ecol 47:243–250

Parolin P, Müller E, Junk WJ (2008) Sapwood area in seven common tree species of Central Amazon floodplains. Pesqui Botân 59:277–286

Parolin P, Lucas C, Piedade MTF, Wittmann F (2010) Drought responses of extremely flood tolerant trees of Amazonian floodplains. Annal Bot 105(1):129–139

Parolin P, Waldhoff D, Piedade MTF (2010a) Gas exchange and photosynthesis. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Parolin P, Waldhoff D, Piedade MTF (2010b) Fruit and seed chemistry, biomass and dispersal. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Parolin P, Wittmann F, Schöngart J (2010c) Tree phenology in Amazonian floodplain forests. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Parotta JA, Francis JK, Almeida RR (1995) Trees of the Tapajós. A photographic field guide. Gen. Tech. Rep. IITF-1. Rio Pedras, PR. U.S. department of agriculture, Forest service, International Institute of Tropical Forestry, USA

Payne L (1991) The alkaloids of *Erythrina:* clonal evaluation and metabolic fate. Ph.D. thesis, Department of Chemistry, Louisiana State University, p 160

Paz H (2003) Root/shoot allocation and root architecture in Seedlings: variation among forest sites, microhabitats and ecological groups. Biotropica 35(3):318–332

Peacock J, Baker TR, Lewis SL, Lopez-Gonzalez G, Phillips OL (2007) The RAINFOR database: monitoring forest biomass and dynamics. J Veg Sci 18:535–542

Peart MH (1981) Further experiments on the biological significance of the morphology of seed-dispersal units in grasses. J Ecol 69:425–436

Peixoto JMA (2007) Monitoramento da dinâmica da geomorfologia fluvial da Reserva de Desenvolvimento Sustentável Mamirauá, por meio de técnicas de sensoriamento remoto. M. Sc. thesis INPA/UFAM, Manaus, Brazil

Penning de Vries FWT (1975) The cost of maintenance processes in plant cells. Ann Bot 39:77–92

Peralta N (2005) Os ecoturistas estão chegando: Aspectos da mudança social na RDS Mamirauá. M.Sc. thesis, Federal University of Pará, Brazil

Peres C (1991) Seed predation of *Cariniana micrantha* (Lecythidaceae) by brown capuchin monkeys in Central Amazonia. Biotropica 23:262–270

Persson T, Rudebeck A, Jussy JH, Colin-Belgrand M, Priemé A, Dambrine E, Karlsson PS, Sjöberg RM (2000) Soil nitrogen turnover – mineralisation, nitrification and denitrification in European forest soils. In: Schulze ED (ed) Carbon and nitrogen cycling in European forest ecosystems. Springer, Berlin/Heidelberg, pp 297–331

Petermann P (1997) The birds. In: Junk WJ (ed) The Central Amazon floodplain. Ecology of a pulsing system. Springer, Berlin/Heidelberg/New York, pp 419–452

Peters CM, Gentry AH, Mendelsohn RO (1989) Valuation of an Amazonian rainforest. Nature 339:655–656

Peterson CA (1997) The exodermis and its interactions with the environment. In: Flores HE, Lynch JP, Eissenstat D (eds) Radical biology: advances and perspectives on the function of plant roots. American Society of Plat Physiologists

Pezeshki SR (1991) Root responses of flood-tolerant and flood-sensitive tree species to soil redox conditions. Trees 5:180–186

Phillips LM, Hayman DS (1970) Improved procedures for clearing roots and staining parasitic and VA-Mycorrhiza fungi for rapid assessment of infection. Trans Br Mycol Soc 55:158–160

Phillips N, Bond BJ, Ryan MG (2001) Gas exchange and hydraulic properties in the crowns of two tree species in a Panamanian moist forest. Trees 15:123–130

Phillips O, Gentry AH (1993) The useful plants of Tambopata, Peru. I: statistical hypothesis tests with a new quantitative technique. Econom Bot 47:15–32

Phillips O, Gentry AH, Wilkin P, Gálvez-Durand C (1994) Quantitative ethnobotany and Amazonian conservation. Conserv Biol 8(1):225–248

Phillips OL, Malhi Y, Higuchi N, Laurance WF, Núñez Vargas P, Vásquez Martinez R, Laurance SG, Ferreira LV, Stern M, Brown S, Grace J (1998) Changes in the carbon balance of tropical forests: evidence of long-term plots. Science 282:439–442

Phillips OL, Malhi Y, Vinceti B, Baker T, Lewis LS, Higuchi N, Laurance WF, Núñez Vargas P, Vásquez Martinez R, Laurance SG, Ferreira LV, Stern M, Brown S, Grace J (2002) Changes in growth of tropical forests: evaluating potential biases. Ecol Appl 12:576–587

Phillips OL, Lewis SL, Baker TR, Chao K-J, Higuchi N (2008) The changing Amazon forest. Philos T Roy Soc B 363:1819–1827

Pianka ER (1970) On r- and K-selection. Nature 104:592–597

Piedade MTF (1985) Ecologia e biologia reprodutiva de *Astrocaryum jauari* Mart. (Palmae) como exemplo de populaçao adaptada as áreas inundáveis do rio Negro. Unpublished Master thesis INPA, Manaus

Piedade MTF, Junk WJ, Long SP (1991) The productivity of the C_4 grass *Echinochloa polystachia* on the Amazon Floodplain. Ecology 72(4):1456–1463

Piedade MTF, Long SP, Junk WJ (1994) Leaf and canopy photosynthetic CO_2 uptake of a stand of *Echinochloa polystachya* on the Central Amazon floodplain. Are the high potential rates associated with the C_4 syndrome realized under the near-optimal conditions provided by this exceptional natural habitat? Oecologia 97:193–201

Piedade MTF, Junk WJ, Parolin P (2000) The flood pulse and photosynthetic response of trees in white water floodplain (várzea) of the Central Amazon, Brazil. Verh Internt Verein Limnol 27(4):1734–1739

Piedade MTF, Worbes M, Junk WJ (2001) Geo-ecological controls on elemental fluxes in communities of higher plants in Amazonian floodplains. In: McClain ME, Victoria RL, Richey JE (eds) The biogeochemistry of the Amazon basin. Oxford University Press, New York, p 209–234

Piedade MTF, Parolin P, Junk WJ (2003) Estratégias de dispersão, produção de frutos e extrativismo da palmeira *Astrocaryum jauari* Mart. nos igapós do Rio Negro: implicações para a ictiofauna. Ecología Aplicada 2:31–40

Piedade MTF, Parolin P, Junk WJ (2006) Phenology, fruit production and seed dispersal of *Astrocaryum jauari* (Arecaceae) in Amazonian black-water floodplains. Revista de Biologia Tropical 54:1171–1178

Piedade MTF, Ferreira CS, Oliveira Wittmann A de, Buckeride M, Parolin P (2010) Biochemistry of Amazonian floodplain trees. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Pigliucci M, Kolodynska A (2002) Phenotypic plasticity and integration in response to flooded conditions in natural accessions of *Arabidopsis thaliana* (L.) Heynh (Brassicaceae). Annal Bot 90:199–207

Pijl L van der (1982) Principles of seed dispersal in higher plant, 3rd edn. Springer, Berlin

Pinedo-Vásquez M, Zarin D, Jipp P, Chota-Inuma J (1990) Use values of tree species in a communal forest reserve in northeast Peru. Conserv Biol 4:405–416

Pires A (2004) Princípios e processos na implantação do manejo florestal comunitário na RDS Mamirauá. In: Ricardo F (ed) Terras indígenas e unidades de conservação da natureza: O desafio das sobreposições. ISA – Instituto Sócio Ambiental, São Paulo, Brazil, pp 558–563

Pires A, Moura E, Disconzi G, Benchimol AS (2001) O desafio de conservar as florestas inundáveis amazônicas no Brasil. In: Carbonell M, Nathai-Gyan N, Finlayson CM (eds) Science and local communities. Ducks Unilimited, Memphis, USA, pp 14–18

Pires JM, Koury HM (1959) Estudo de um trecho de mata de várzea próximo a Belém. Boletim Técnico IAN 36:3–44

Pires JM (1961) Esboço fitogeografico da Amazonia. Rev Soc Agron Vet Pará 7:3–8

Pires JM (1984) The Amazonian forest. In: Sioli H (ed) The Amazon – limnology and landscape ecology of a mighty tropical river and its basin. Junk, Dordrecht, pp 581–602

Pires JM, Prance GT (1985) The vegetation types of the Brazilian Amazon. In: Prance GT, Lovejoy TE (eds) Key environments: Amazonia. Pergamon, Oxford, pp 109–145

Pisarz M (1995) Untersuchungen zum Vorkommen bestimmter Tierseuchen bei Rindern und Wasserbüffeln in den Weisswasser-Überschwemmungsgebieten (Várzeas) der mittleren Amazonasregion Brasiliens. Ph.D. thesis, University Gießen, Germany

Pitman NCA, Terborgh J, Silman MR, Núñez PV, Neill DA, Cerón CE, Palacios WA, Aulestia M (2001) Dominance and distribution of tree species in upper Amazonian terra firme forests. Ecology 82:2101–2117

Pitman NCA, Terborgh J, Silman MR, Nuñez PV, Neill DA, Cerón CE, Palacios WA, Aulestia M (2002) A comparison of tree species diversity in two upper Amazonian forests. Ecology 83(11):3210–3224

Plitmann U (1986) Alternative modes in dispersal strategies, with emphasis on herbaceous plants of the Middle East. Proc Roy Soc Edinburgh 89B:193–202

Plumel MM (1991) Le genre *Himatanthus* (Apocynaceae). Révision taxonomique. Bradea 5:118

Ponnamperuma FN (1984) Effects of flooding on soils. In: Kozlowski TT (ed) Flooding and plant growth. Academic Press, London, pp 9–45

Pons TL (2000) Seeds responses to light. In: Fenner M (ed) Seeds the ecology of regeneration in plant communities, 2nd edn. CABI publishing, Wallingford, pp 237–260

Porro A (1996) O povo das águas: ensaios de etno-história Amazônica. Edusp/Vozes, Petrópolis, Brazil

Potomati A, Buckeridge MS (2002) Effect of abscisic acid on the mobilisation of galactomannan and embryo development of *Sesbania virgata* (Cav) Pers. (Leguminosae – Faboideae). Revista Brasileira de Botânica 25(3):303–310

Pouilly M, Beck SG, Moraes M, Ibañez R, Ibañez C (eds) (2004) Diversidad Biológica en la Llanura de Inundación del Río Mamoré: Importancia ecológica de la Dinámica Fluvial. Centro de Ecología Simón I, Patiño, Santa Cruz, Bolivia

Prance GT (1973) Phytogeographic support to the theory of Pleistocene forest refuges in the Amazon basin. Acta Amazonica 3:5–28

Prance GT (1979) Notes on the vegetation of Amazonia. 3. The terminology of Amazonian forest types subject to inundation. Brittonia 31:26–38

Prance GT (1982) Biological diversity in the tropics. Columbia University Press, New York

Prance GT (1987) Vegetation. In: Whitmore TC, Prance GT (eds) Biogeography and quaternary history in tropical America. Clarendon Press, Oxford, pp 28–44

Prentice IC, Lloyd J (1998) C-quest in the Amazon Basin. Nature 396:619–620

Pressey RL, Albernaz AL, Scaramuzza CAM (2005) A spatial framework for conservation planning in the varzea floodplains of the Brazilian Amazon. Soc Conserv Biology Ann Mtg, Brasilia. http://www.conbio.org/Activities/Meetings/2005/pdf/abstract.pdf

Pretto JB, Cechinel-Filho V, Noldin VF, Sartori MRK, Isaias DEB, Cruz AB (2004) Antimicrobial activity of fractions and compounds from *Calophyllum brasiliense* (Clusiaceae/Guttiferae). Z Naturforsch 59c:657–662

Pretzsch H (2001) Modellierung des Waldwachstums. Parey Buchverlag, Berlin

Price TD, Qvarnstrom A, Irwin DE (2003) The role of phenotypic plasticity in driving genetic evolution. Proceedings of the Royal Society of London, series B, vol 270, pp 1433–1440

Price JP, Elliot-Fisk D (2004) Topographic history of the Maui Nui Complex, Hawai’i, and its implications for biogeography. Pacific Sci 58(1):27–45

Priess J, Then C, Fölster H (1999) Litter and fine root production in three types of tropical premontane rain forest in SE Venezuela. Plant Ecol 143:171–187

Projeto Radam (1970–1972) Mosaico semi controlado de Radar. Ministério das Minas e Energia, Departamento Nacional da Produção Mineral

Projeto RADAMBRASIL (1978) Folha SA.20 Manaus: geologia, geomorfologia, pedologia, vegetação e uso potencial da terra. Departamento Nacional da Produção Mineral, Rio de Janeiro

Puhakka M, Kalliola R (1993) La vegetación en áreas de inundación en la selva baja de la Amazonia Peruana. In: Kalliola R, Puhakka M, Danjoy W (eds) Amazonia Peruana: Vegetación húmeda tropical en el llano subandino. Proyecto Amazonia, Turku, pp 113–138

Puhakka M, Kalliola R, Rajasilta M, Salo J (1992) River types, site evolution and successional vegetation patterns in Peruvian Amazonia. J Biogeogr 19:651–665

Putz FE, Sist P, Fredericksen T, Dykstra D (2008) Reduced-impact logging: challenges and opportunities. Forest Ecol Manag 256:1427–1433

Queiroz HL (1994) Uma experiência de conservação na várzea da Amazônia brasileira. Neotrop Primates 2(1):12–13

Queiroz HL (1995) Preguiças e Guaribas: os Mamíferos Folívoros Arborícolas doMamirauá. MCT/CNPq, Sociedade Civíl Mamirauá, Brasília

Queiroz HL (1997) Artisanal fisheries of pirarucu at the Mamirauá Ecological Station. In: Padoch C, Ayres JM, Pinedo-Vasquez M, Henderson A (eds) Várzea: diversity, development, and conservation of Amazonia’s whitewater floodplains. The New York Botanical Garden Press, New York, pp 83–100

Queiroz HL (2000) Natural history and conservation of pirarucu, *Arapaima gigas*, at the Amazonian várzea: red giants in muddy waters. Ph.D. thesis, School of Environmental and Evolutionary Biology, University of St. Andrews

Queiroz HL (2005a) A pesquisa científica em Mamirauá: Instrumento de consolidação do manejo participativo e da conservação da biodiversidade. In: Fany R (ed) Terras indígenas e unidades de conservação da natureza: O desafio das sobreposições. Instituto Sócio Ambiental, São Paulo, SP, pp 542–549

Queiroz HL (2005b) A RDSM - um modelo de área protegida de uso sustentável. Estudos Avançados – Dossiê Amazônia, São Paulo 54(2):183–204

Queiroz HL, Crampton W (1999) Estratégias para Manejo dos Recursos Pesqueiros em Mamirauá. SCM, CNPq/MCT, Brasília, DF

Queiroz HL, Sardinha AD (1999) A preservação e o uso sustentado dos pirarucus (Arapaima gigas, Osteoglossidae) em Mamirauá. In: Queiroz HL, Crampton W (eds) Estratégias para manejo de recursos pesqueiros em Mamirauá. SCM, CNPq/MCT, Brasília, pp 108–141

Queiroz HL, Fernandes MEB (2001) A proposal for the establishment of a natural world heritage site and cultural landscape world heritage site – a new world heritage site: the Central Amazon Protected Areas. Report to the Brazilian Ministry of Environment and to UNESCO, Brasília

Queiroz HL, Peralta N (2006) Reservas de Desenvolvimento Sustentável: Manejo integrado de recursos naturais e gestão participativa. In: Gatay I, Becker B (eds) Dimensões humanas da biodiversidade. Editora Vozes, Petrópolis

Queiroz HL, Peralta N (2009) Protected areas in the Amazonian várzea and their role in its conservation: The case of Mamirauá Sustainable Development Reserve (MSDR). In: Junk WJ, Piedade MTF, Parolin P, Wittmann F, Schöngart J (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Queiroz HL, Peralta N (2010) Protected areas in Amazonian várzea and their role in its conservation: the case of Mamirauá Sustainable Development Reserve (MSDR). In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Räsanen M (1993) La geohistoria y geología de la Amazonia peruana. In: Kalliola R, Puhakka M, Danjoy W (eds) Amazonia Peruana – Vegetacion humeda tropical en el llano subandino. Gummerus Printing, Jyväskylä, pp 43–68

Rätsch G, Haase K (2007) Internal root aeration and anatomic prerequisites of three tree species of the Amazonian inundation forest. Amazoniana 19:185–197

Redhead JF (1980) Mycorrhiza in natural tropical forests. In: Mikola P (ed) Tropical Mycorrhiza research. Clarendon Press, Oxford, pp 127–142

Rehm S, Espig G (1976) Die Kulturpflanzen der Tropen und Subtropen. Ulmer, Stuttgart

Reich PB, Borchert R (1982) Phenology and ecophysiology of the tropical tree*, Tabebuia neochrysantha* (Bignoniaceae). Ecology 63(2):294–299

Reich PB, Borchert R (1984) Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. J Ecol 72:61–74

Reis M (2003) Arengas e psicas. As reações populares à criação da RDS Mamirauá e ao manejo sustentável e participativo dos recursos naturais. M.Sc. Thesis, Instituto de Ciências Humanas e Sociais Departamento de Desenvolvimento, Agricultura e Sociedade, Federal Rural University of Rio de Janeiro

Revilla JDC (1981) Aspectos Florísticos e Fitossociológicos da Floresta Inundável (igapó). Praia Grande, Tio Negro, Amazonas. Master thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus

Revilla JDC (1991) Aspéctos florísticos e estruturais da floresta inundável (várzea) do baixo Solimões, Amazonas, Brasil. Doctoral Thesis, INPA, Manaus, pp 151

Revsbech NP, Pedersen O, Reichardt W, Briones A (1999) Microsensor analysis of oxygen and pH in the rice rhizosphere under field and laboratory conditions. Biol Fertil Soils 29:379–385

Reyes-García V, Huanca T, Vadez V, Leonard W, Wilkie D (2006) Cultural, practical, and economic value of wild plants: a quantitative study in the Bolivian Amazon. Econom Bot 60(1):1–13

Ribeiro JE, Hopkins M, Vicentini A, Sothers CA, Costa MA, Brito JM, Souza MA, Martins LH, Lohmann LG, Assunção PA, Pereira E, Silva CF, Mesquita MR, Procópio LC (1999) Flora da Reserva Ducke Guia de identificacão das plantas vasculares de uma floresta de terra firme na Amazônia Central. INPA-DFID, Manaus

de Ribeiro MNG, Adis J (1984) Local rainfall variability – a potential bias for bioecological studies in the central Amazon. Acta Amazonica 14:159–174

Richards PW (1952) The tropical rain forest. Cambridge University Press, London

Richards PW (1996) The tropical rainforest, 2nd edn. Cambridge University Press, Cambridge

Richey JE, Nobre CA, Deser C (1989) Amazon river discharge and climate variability: 1903–1985. Science 246:101–103

Richey JE, Melack JM, Aufdenkampe AK, Ballester VM, Hess LL (2002) Outgassing from Amazonian rivers and wetlands as a large tropical source of atmospheric CO_2. Nature 416: 617–620

Ricklefs RE (1990) Ecology. WH Freeman, New York

Ridley HN (1930) The dispersal of plants throughout the world. L Reeve, Ashford, Kent

Rieseberg LH, Wendel J (2004) Plant speciation – rise of the poor cousins. New Phytol 161(1):3–8

Rivera G, Elliott S, Caldas LS, Nicolossi G, Coradin VTR, Borchert R (2002) Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. Trees 16:445–456

Rizzini CT (1997) Tratado de fitogeografia do Brasil, aspectos ecológicos, sociológicos e florísticos. EDUSP, Rio de Janeiro

Roberts J, Cabral OMR, Aguiar LFD (1990) Stomatal and boundary-layer conductances in Amazonian terra firme rain forest. J Appl Ecol 27:336–353

Robertson C (1895) The philosophy of flower seasons, and the phenological relations of the entomophilous flora and the anthophilous insect fauna. Am Nat 29:97–117

Roças G, Scarano FR, Barros CF (2001) Variation in leaf anatomy of *Alchornea triplinervia* (Spreng) Müll Arg (Euphorbiaceae) under different light and soil-water regimes. Botan J Linn Soc 136:231–238

Roddaz M, Baby P, Brusset S, Hermoza W, Darrozes JM (2005) Forebulge dynamics and environmental control in western Amazonia: the case study of the Arch of Iquitos (Peru). Tectonophysics 399:87–108

Rodrigues RR (2000) Uma discussão nomenclatural das formações ciliares. In: Rodrigues RR, Leitão Filho H de F (eds) Matas ciliares: conservação e recuperação. EDUSP, FAPESP, São Paulo, pp 91–99

Rodrigues WA (1961) Estudo preliminar de mata de várzea alta de uma ilha do baixo Rio Negro de solo argiloso e umido. Publicação número 10 do Instituto Nacional de Pesquisas da Amazônia, Manaus

Roggy JC, Prevost MF, Garbaye J, Domenach AM (1999a) Nitrogen cycling in the tropical rain forest of French Guiana: comparison of two sites with contrasting soil types using δ^{15}N. J Trop Ecol 15:1–22

Roggy JC, Prevost MF, Gourbiere F, Casabianca H, Garbaye J, Domenach AM (1999b) Leaf natural ^{15}N abundance and total N concentration as potential indicators of plant N nutrition in legumes and pioneer species in a rain forest of French Guiana. Oecologia 120:171–182

Rohling EJ, Grant K, Hemleben CH, Siddall M, Hoogakker BAA, Bolshaw M, Kucera M (2008) High rates of sea-level rise during the last interglacial period. Nature Geoscience vol 1. Heft 1:38–42

Rollenbeck R, Anhuf D (2007) Characteristics of the water and energy balance in an Amazonian lowland rainforest in Venezuela and the impact of the ENSO-cycle. J Hydrol 337:377–390

Ronchail J, Labat D, Callède J, Cochonneau G, Guyot JL, Filizola N, Oliveira E (2005) Discharge variability within the Amazon basin. In: Franks J, Wagener T, Bogh E, Gupta HV, Bastidas L, Nobre C, Galvão CO (eds) Regional hydrological impacts of climatic changes. Hydroclimatic variability, vol 296, pp 21–30. IAHS Publications

Roosevelt AC (1999) Twelve thousand years of human-environment interaction in the Amazon Floodplain. In: Padoch C, Ayres JM, Pinedo-Vasquez M, Henderson A (eds) Várzea: diversity, development, and conservation of Amazonia's whitewater floodplains. The New York Botanical Garden Press, New York, pp 371–392

Roosevelt AC, Housley RA, Imazio da Silveira M, Maranca S, Johnson R (1991) Eighth millennium pottery from a prehistoric shell midden in the Brazilian Amazon. Science 254:1621–1624

Rosa SA (2008) Modelos de crescimento de quatro espécies madeireiras de floresta de várzea alta da Amazônia Central por meio de métodos dendrocronológicos. M.Sc. thesis INPA/UFAM, Manaus, Brazil

Rosales J, Petts G, Knab-Vispo C (2001) Ecological gradients in riparian forests of the lower Caura River, Venezuela. Plant Ecol 152(1):101–118

Rosales J, Vispo C, Dezzeo N, Blanco-Belmonte L, Knap-Vispo, Gonzalez N, Daza F, Bradley C, Gilvear D, Escalante G, Chacón N, Petts G (2002) Ecohydrology of riparian forests in the Orinoco River basin. In: the ecohydrology of South-American rivers and wetlands. IAHS Special Publication no 6, pp 93–110

Rosenqvist A, Shimada M, Chapman B, Freeman A, Grande G, Saatchi S, Rauste Y (2000) The global rain forest mapping project – a review. Int J Remote Sens 21:1375–1387

Ros-Tonen MAF (1993) Tropical hardwood from the Brazilian Amazon. Verlag Breitenbach Publishers, Saarbrücken-Fort Lauterdale

Roth I (1984) Stratification of tropical forests as seen in leaf structure. Junk Publishers, The Hague

Rottenberger S (2003) Exchange of oxygenated volatile organic compounds between Amazonian and European vegetation and atmosphere. Ph.D. thesis, University of Mainz

Rottenberger S, Kleiss B, Kuhn U, Wolf A, Piedade MTF, Junk J, Kesselmeier J (2008) The effect of flooding on the exchange of the volatile C2-compounds ethanol, acetaldehyde and acetic acid between leaves of Amazonian floodplain tree species and the atmosphere. Biogeosciences (Katlenburg-Lindau) (5):1085–1100

Roubach R (1995) Growth performance of *Colossoma macropomum* (Serrasalminae) fed with fruits from inundated forests. In: 2nd SHIFT Workshop Cuiabá, Genus Ed, pp 52–53

Rovinski JM, Gregory LT, Sneden AT (1987) Maquiroside A, a new cytotoxic cardiac glycoside from *Maquira calophylla*. J Nat Prod 50(2):211–216

Roy J, Saugier B, Mooney HA (2001) Terrestrial global poroductivity. Academic Press, San Diego, California

Rubio G, Casasola G, Lavado RS (1995) Adaptations and biomass production of two grasses in response to waterlogging and soil nutrient enrichment. Oecologia 102:102–105

Rudorff C, Novo EMLM, Galvão L (2006) Spectral mixture analysis of inland tropical Amazon floodplain waters using EO-1 Hyperion. Proceedings, IGARSS ‘06. IEEE, Denver Pages, pp 128–133

Ruffino ML (1996) Towards participatory fishery management on the lower Amazon. EC Fish Cooperat Bull 9(1):15–18

Rull V (1999) Palaeofloristic and palaeovegetational changes across the Paleocene-Eocene boundary in northern South America. Rev Palaeobot Palynol 107:83–95

Ruokolainen K, Schulman L, Tuomisto H (2001) On Amazon peatlands. IMCG Newslett 2001(4):8–10

Ryan MG, Hubbard RM, Clark DA, Sanford RL Jr (1994) Woody-tissue respiration for *Simarouba amara* and *Minquartia guianensis*, two tropical wet forest trees with different growth habits. Oecologia 100:213–220

Ryan MG, Gowe ST, Hubbard RM, Waring RH, Gholz HL, Cropper WP Jr, Running SW (1995) Woody tissue maintenance respiration of four conifers in contrasting climates. Oecologia 101:133–140

Saatchi SS, Nelson B, Podest E, Holt J (2000) Mapping land cover types in the Amazon Basin using 1 km JERS-1 mosaic. Int J Remote Sens 21:1201–1234

Saatchi SS, Houghton RA, Alvalá RCS, Soares JV, Yu Y (2007) Distribution of aboveground live biomass in the Amazon basin. Global Change Biol 13:813–837

Sahagian D, Melack JM (1998) Global wetland distribution and functional characterization: trace gases and the hydrologic Cycle. IGPB Report 46. IGBP Secretariat, Royal Swedish Academy of Sciences, Stockholm, Sweden

Saint-Paul U (1982) Ökologische und physiologische Untersuchungen an dem Amazonasfisch Tambaqui *Colossoma macropomum* (Cuvier 1818) im Hinblick auf seine Eignung für die tropische Fischzucht (Pisces, Serrasalmidae). Unpublished Ph.D. Thesis, Univ Hamburg

Saint-Paul U, Soares MGM (1995) The Amazonian inundated forest: relation between fish and environment. In: 2nd SHIFT Workshop Cuiabá, Genus Ed, pp 41–43

Saint-Paul U, Zuanon J, Correa MAV, Carcía M, Fabré NN, Berger U, Junk WJ (2000) Fish communities in central Amazonian white- and blackwater floodplains. Environ Biol Fish 57:235–250

Saitou N, Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. Molecul Biol Evolut 4:406–425

Sakai S, Momose K, Yumoto T, Nagamitsu T, Nagamasu H, Hamid AA, Nakasiiizuka T (1999) Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarwak, Malaysia. Am J Bot 86:1414–1436

Salati E, Sylvester-Bradley R, Victoria RL (1982) Regional gains and losses of nitrogen in the Amazon basin. Plant Soil 67:367–376

Saldarriaga JG (1987) Recovery following shifting cultivation. A century of succession in the upper Rio Negro. In: Jordan CF (ed) Amazonian rain forests: ecosystem disturbance and recovery. Springer, New York, pp 24–33

Saldarriaga JG, West DC, Tharp ML, Uhl C (1988) Long-term chronosequence of forest succession in the upper Rio Negro of Columbia and Venezuela. J Ecol 76:938–958

Saleska SR, Miller SD, Matross DM, Goulden ML, Wofsy SC, Rocha HR, Camargo PB, Crill P, Daube BC, Freitas HC, Hutyra L, Keller M, Kirchoff V, Menton M, Munger JW, Pyle EH, Rice AH, Silva H (2003) Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. Science 302:1554–1557

Salisbury EJ (1942) The reproductive capacity of plants. Bell, London, p 216

Salo J, Kalliola R, Häkkinen L, Mäkinen Y, Niemelä P, Puhakka M, Coley PD (1986) River dynamics and the diversity of Amazon lowland forest. Nature 322:254–258

Sanford RL (1989) Root system of three adjacent, old growth Amazon forests and associated transition zones. J Trop For Sci 1:268–279

Sanford RL, Saldarriaga J, Clark KE, Uhl C, Herrera R (1985) Amazon rain-forest fires. Science 227:53–55

Sangakkara UR, Hartwig UA, Nösberger J (1996) Soil moisture and potassium affect the performance of symbiotic nitrogen fixation in faba bean and common bean. Plant Soil 184:123–130

Santiago EF, Paoli AS (2007) Morphological responses in *Guibourtia hymenifolia* (Moric.) J. Leonard (Fabaceae) and *Genipa americana* L. (Rubiaceae) to nutrient deficit and flooding stress. Revista Brasileira de Botanica 30(1)

Santos GM dos (1986/1987) Composição do pescado e situação da pesca no Estado de Rondônia. Acta Amazônica 16/17 (Supl.):43–84

Santos R (1980) História econômica da Amazônia (1800–1920). TA Queiroz, São Paulo

Santos SRM, Miranda IS, Tourinho MM (2004) Análise floristica e estrutural de sistemas agroflorestais das várzeas do Rio Juba, Cametá, Pará. Acta Amazônica 34(2):251–263

Saraiva NAM (2003) Diagnostico da Piscicultura na área de expansão do Districo Federal. Monografia DEPESCA-UFAM, Brasília, Brazil

Saravy FP, Fretas PJ, Lage MA, Leite SJ, Braga LF (2003) Síndrome de dispersao em estratos arbóreos em um fragmento de floresta ombrófila aberta e densa em alta floresta – MT Revista do Programa de Ciências Agro-Ambientais. Alta Floresta 2:1–12

Sayer EJ, Tanner EVJ, Cheesman AW (2006) Increased litterfall changes fine root distribution in a moist tropical forest. Plant Soil 281:5–13

Scarano FR (1998) A comparison of dispersal, germination and establishment of woody plants subjected to distinct flooding regimes in Brazilian flood-prone forests and estuarine vegetation. In: Scarano FR, Franco AC (eds) Ecophysiological strategies of xerophytic and amphibious plants in the neotropics. Series Oecologia Brasiliensis, vol IV. PPGE – UFRJ. Rio de Janeiro, Brazil. pp 177–193

Scarano FR, Cattânio JH, Crawford RMM (1994) Root carbohydrate storage in young saplings of an Amazonian tidal várzea forest before the onset of the wet season. Acta Botanica Brasilica 8(2):129–139

Scarano FR, Pereira TS, Rocas G (2003) Seed germination during floatation and seedling growth of *Carapa guianensis*, a tree from flood-prone forests of the Amazon. Plant Ecol 168(2):291–296

Scherfose V (1990) Feinwurzelverteilung und Mykorrhizatypen von *Pinus sylvestris* in verschiedenen Bodentypen. Berichte des Forschungszentrums Waldökosysteme Göttingen, Reihe A, Bd 62, p 166

Schimel DS, House JI, Hibbard KA, Bousquet P, Ciais P, Peylin P, Braswell BH, Apps MJ, Baker D, Bondeau A, Canadell J, Churkina G, Cramer W, Denning AS, Field CB, Friedlingstein P, Goodale C, Heimann M, Houghton RA, Melillo JM, Moore B III, Murdiyarso D, Noble I, Pacala SW, Prentice IC, Raupach MR, Rayner PJ, Scholes RJ, Steffen WL, Wirth C (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature 414:169–172

Schlichting E, Blume H-P, Stahr K (1995) Bodenkundliches Praktikum, 2nd edn. Blackwell Wissenschaftsverlag, Berlin

Schlüter U-B (1989) Morphologische, anatomische und physiologische Untersuchungen zur Überflutungstoleranz zweier charakteristischer Baumarten (Astrocaryum jauari und Macrolobium acaciaefolium) des Weiss- und Schwarz-wasserüberschwemmungswaldes bei Manaus.- ein Beitrag zur Ökosystemanalyse von Várzea und Igapó Zentralamazoniens. Ph.D. Thesis, University of Kiel, Germany

Schlüter UB, Furch B (1992) Morphologische, anatomische und physiologische Untersuchungen zur Überflutungstoleranz des Baumes *Macrolobium acaciaefolium*, charakteristisch für die Weißund Schwarzwasser-Überschwemmungswälder bei Manaus, Amazonas. Amazoniana 12:51–69

Schlüter UB, Furch B, Joly CA (1993) Physiological and anatomical adaptations by young *Astrocaryum jauari* Mart (Arecaceae) in periodically inundated biotopes of Central Amazonia. Biotropica 25(4):384–396

Schnitzler A, Hale BW, Alsum E (2005) Biodiversity of floodplain forests in Europe and eastern North America: a comparative study of the Rhine and Mississippi valleys. Biodivers Conserv 14:97–117

Scholander PF, Perez MO (1968) Sap tension in flooded trees and bushes of the Amazon. Plant Physiol 43:1870–1873

Scholz F, Bucci SJ, Goldstein G, Meinzer F, Franco AC, Miralles-Wilhelm F (2007) Biophysical properties and functional significance of stem water storage tissues in Neotropical savanna trees. Plant Cell Environ 30:236–248

Schöngart J (2003) Dendrochronologische Untersuchungen in Überschwemmungswäldern der várzea Zentralamazoniens. Göttinger Beiträge zur Land- und Forstwirtschaft in den Tropen und Subtropen 149, Erich Goltze Verlag, Göttingen

Schöngart J (2008) Growth-Oriented Logging (GOL): a new concept towards sustainable forest management in Central Amazonian várzea floodplains. Forest Ecol Manag 256:46–58

Schöngart J (2010) Growth-Oriented Logging (GOL): The Use of Species-Specific Growth Information for Forest Management in Central Amazonian Floodplains. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Schöngart J, Junk WJ (2007) Forecasting the flood-pulse in Central Amazonia by ENSO-indices. J Hydrol 335:124–132

Schöngart J, Piedade MTF, Ludwigshausen S, Horna V, Worbes M (2002) Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. J Trop Ecol 18:581–597

Schöngart J, Piedade MTF, Worbes M (2003) Successional differentiation in structure, floristic composition and wood increment of whitewater floodplain forests in Central Amazonia. In: Lieberei R, Bianchi HK, Boehm V, Reissdorf C (eds) Neotropical ecosystems – proceedings of the German-Brazilian workshop Hamburg, 2000. GKSS Geesthacht, pp 589–606

Schöngart J, Junk WJ, Piedade MTF, Ayres JM, Hüttermann A, Worbes M (2004) Teleconnection between tree growth in the Amazonian floodplains and the El Niño-Southern oscillation effect. Global Change Biol 10:683–692

Schöngart J, Piedade MTF, Wittmann F, Junk WJ, Worbes M (2005) Wood growth patterns of *Macrolobium acaciifolium* (Benth.) Benth. (Fabaceae) in Amazonian black-water and white-water floodplain forests. Oecologia 145:654–661

Schöngart J, Orthmann B, Hennenberg KJ, Porembski S, Worbes M (2006) Climate-growth relationships of tropical tree species in West Africa and their potential for climate reconstruction. Global Change Biol 12:1139–1150

Schöngart J, Wittmann F, Worbes M, Piedade MTF, Krambeck H-J, Junk WJ (2007) Management criteria for *Ficus insipida* Willd. (Moraceae) in Amazonian white-water floodplain forests defined by tree-ring analysis. Ann For Sci 64:657–664

Schöngart J, Queiroz HL (2010) Timber extraction in the Central Amazonian floodplains. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Schöngart J, Wittmann F, Worbes M (2010) Biomass and NPP of Central Amazonian floodplain forests. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Schreiber L, Hartmann K, Skrabs M, Zeier J (1999) Apoplastic barriers in roots: chemical composition of endodermal and hypodermal cell walls. J Exp Bot 50(337):1267–1280

Schroeder FG (1998) Lehrbuch der Pflanzengeographie. UTB, Wiesbaden, p 457

Schulze ED, Čermak J, Matyssek R, Penka M, Zimmermann R, Vasicek F, Gries W, Kucera J (1985) Canopy transpiration and water fluxes in the xylem of the trunk of *Larix* and *Picea* trees – A comparison of xylem flow, porometer and cuvette measurements. Oecologia 66:475–483

Schulze ED, Kelliher FM, Körner C, Lloyd J, Leuning R (1994) Relationship among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: a global ecology scaling exercise. Annu Rev Ecol Syst 25:629–660

Schwartz MW, Caro TM, Banda-Sakala T (2002) Assessing the sustainability of harvest of *Pterocarpus angolensis* in Rukwa Region, Tanzania. Forest Ecol Manag 170:259–269

Schweingruber FH (1996) Tree rings and environment. Dendroecology. Birmensdorf, Swiss Federal Institute for Forest, Snow and Landscape Research, WSL/FNP. Berne, Stuttgart, Vienna

Schweingruber FH (2001) Dendroökologische Holzanatomie. Anatomische Grundlagen der Dendrochronologie. Eidg. Forschungsanstalt WSL, Paul Haupt, Bern

Schweingruber FH, Bräker OU, Schär E (1978) X-ray densitometric results for subalpine conifers and their relationship to climate. In: Fletcher J (ed) Dendrochronology in Europe. British archaeological reports, International Series 51:89–100

Seaton GR, Walker DA (1992) Validating chlorophyll fluorescence measures of efficiency: observations on fluorimetric estimation of photosynthetic rate. Proc R Soc Lond B 249:41–47

Sebbenn AM, Degen B, Azevedo VCR, Silva MB, Lacerda AEB, Ciampi AY, Kanashiro M, Carneiro FS, Thompson I, Loveless MD (2008) Modelling the long-term impacts of selective logging on genetic diversity and demographic structure of four tropical tree species in the Amazon fores. Forest Ecol Manag 254:335–349

Seghieri J, Floret C, Pontanier R (1995) Plant phenology in relation to water availability: herbaceous and woody species in the savannas of northern Cameroon. J Trop Ecol 11:237–254

Seigler DS (2005) Cyanogenic glycosides and menisdaurin from *Guazuma ulmifolia, Ostrya virgininana, Tiquilia plicata* and *Tiquilia canescens*. Phytochemistry 66(13):1567–1580

Sena Gomes AR, Kozlowski TT (1988) Stomatal characteristics, leaf waxes, and transpiration rates on *Theobroma cacao* and *Hevea brasiliensis* seedlings. Ann Bot 61:425–432

Sestak Z (1985) Photosynthesis during leaf development. Dr WJunk Publ Dordrecht Boston Lancaster 396 pp

Shanley P, Luz L, Cymerys M (2002) Subsistence issues: the interface of timber and non-timber resources: declining resources for subsistence livelihoods (Brazil). In: Shanley P, Pierce AR, Laird SA, Guillén A (eds) Tapping the green market: certification and management of non-timber forest products. Earthscan, London, pp 313–321

Shearer G, Kohl DH (1986) N_2-fixation in field settings: estimations based on natural ^{15}N abundance. Aust J Plan 13:699–756

Shearer G, Kohl DH (1988) Natural ^{15}N abundance as a method of estimating the contribution of biologically fixed nitrogen to N_2-fixing systems: potential for non-legumes. Plant Soil 110:317–327

Shrimpton R, Giugliano R, Rodrigues NM (1979) Consumo de alimentos e alguns nutrientes em Manaus, 1973-1974. Acta Amazonica 9:117–141

Shuttleworth WJ, Gash JHC, Lloyd CR, Moore CJ, Roberts J, AdO M, Fisch G, VdP SF, Ribeiro MNG, Molion LCB, de Sa LDA, Nobre JC, Cabral OMC, Patel SR, de Moraes JC (1984) Eddy correlation measurements of energy partition for Amazonian forest. Q J R Meteorol Soc 110:1143–1162

Siebel HN, van Wijk M, Blom CWPM (1998) Can tree seedlings survive increased flood levels of rivers? Acta Bot Neerl 47(2):219–230

Silva MF (1977) Nomes vulgares de plantas amazônicas. Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus

Silva MFF (1982) Nota sobre decomposição de materia orgânica em floresta de terra firme, várzea e igapó. M.Sc. thesis, INPA/UFAM, Manaus, Brazil

Silva MFF (1984) Produção de serrapilheira e seu conteúdo minerológico em mata de terra firme, Tucurui (PA). Boletim do Museu Emilio Goeldi (Série Botânica) 1:111–152

Silva RP, Santos J, Tribuzy ES, Chambers JQ, Nakamura S, Higuchi N (2002) Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil. Forest Ecol Manag 166:295–301

Silver WL, Kueppers LM, Lugo AE, Ostertag R, Matzek V (2004) Carbon sequestration and plant community dynamics following reforestation of tropical pasture. Ecol Appl 14:1115–1127

Singer R, Araujo I (1986) Litter decomposition and ectomycorrhizal Basidiomycetes in an igapó Forest. Pl Syst Evol 153:107–117

Singh HB, Kanakidou M, Crutzen PJ, Jacob DJ (1995) High concentrations and photochemical fate of oxygenated hydrocarbons in the global troposphere. Nature 378:50–54

Sioli H (1954a) Beiträge zur regionalen Limnologie des Amazonasgebietes. Archiv für Hydrobiologie 45:267–283

Sioli H (1954b) Betrachtungen über den Begriff "Fruchtbarkeit" eines Gebiets anhand der Verhältnisse in Böden und Gewässern Amazoniens. Forschung Fortschritt 28:65–72

Sioli H (1956) Über Natur und Mensch im brasilianischen Amazonasgebiet. Erdkunde 10(2): 89–109

Sioli H (1957) Sedimentation im Amazonasgebiet. Geol Rundschau 45:608–633

Sioli H (1984a) The Amazon: limnology and landscape ecology of a mighty tropical river and its basin. Dr. W. Junk Publishers, The Netherlands

Sioli H (1984b) The Amazon and its main affluents: hydrography, morphology of the river courses and river types. In: Sioli H (ed) The Amazon. Limnology and landscape ecology of a mighty tropical river and its basin. Dr. W. Junk Publishers, Dordrecht, pp 127–165

Sippel SJ, Hamilton SK, Melack JM, Novo EMLM (1998) Passive microwave observations of inundation area and the area/stage relation in the Amazon River floodplain. Int J Remote Sens 19:3055–3074

Sippel SK, Hamilton SK, Melack JM, Choudhury B (1994) Determination of inundation area in the Amazon River floodplain using the SMMR 37 GHz polarization difference. Remote Sens Environ 48:70–76

Siqueira P, Hensley S, Shaffer S, Hess LL, McGarragh G, Chapman B, Freeman A (2000) A continental-scale mosaic of the Amazon Basin using JERS-1 SAR. IEEE Trans Geosci Remote Sens 38:2638–2644

Sist P, Nolan T, Bertault J-G, Dykstra D (1998) Harvesting intensity versus sustainability in Indonesia. Forest Ecol Manag 108:251–260

Sist P, Picard N, Gourlet-Fleury S (2003) Sustainable cutting cycle and yields in a lowland mixed dipterocarp forest of Borneo. Ann For Sci 60:803–814

Smirnoff N, Crawford RMM (1983) Variation in the structure and response to flooding of root aerenchyma in some wetland plants. Ann Bot 51:237–249

Smith KA, Ball T, Conen F, Dobbie KE, Massheder J, Rey A (2003) Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. European J Soil Science 54:779–791

Smith NJH (1979) A pesca no rio Amazonas. CNPq/INPA, Manaus, Brazil

Smith NJH (1999) The Amazon River Forest: a natural history of plants, animals, and people. Oxford University Press, New York

Smith TB, Schneider CJ, Holder K (2001) Refugial isolation versus ecological gradients. Genetica 112–113:383–398

Smith-Becker J, Marois E, Huguet EJ, Midland SL, Sims JJ, Keen NT (1998) Accumulation of salicylic acid and 4-hydroxybenzoic acid in phloem fluids of cucumber during systemic aquired resistance is preceded by a transient increase in phenylalanine ammonia-lyase activity in petioles and stems. Plant Physiol 116:231–238

Snow DW (1965) A possible selective factor in the evolution of fruiting seasons in tropical forest. Oikos 15:274–281

Snow DW (1981) Tropical frugivorous birds and their food plants: a world survey. Biotropica 13:1–14

Soares-Filho BS, Nepstad DC, Curran LM, Cerqueira GC, Garcia RA, Azevedo Ramos C, Voll E, McDonald A, Lefebvre P, Schlesinger P (2006) Modelling conservation in the Amazon basin. Nature 440:520–523

Sociedade Civíl Mamirauá (1996) Mamirauá: management plan (summarized version). SCM, CNPq/MCT, Brasilía, Brasil

Sokpon N, Biaou SH (2002) The use of diameter distributions in sustained-use management of remnant forests in Benin: case of Bassila forest reserve in North Benin. Forest Ecol Manag 161:13–25

Sombroek W (2001) Spatial and temporal patterns of Amazon rainfall. Ambio 30:388–396

Sørensen T (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. Det Kongelige Danske Videnskabers Selskab Biologiske Skrifter 5(4):1–34

Soukup A, Armstrong W, Schreiber L, Franke R, Votrubová O (2007) Apoplastic barriers to radial oxygen loss and solute penetration: a chemical and functional comparison of the exodermis of two wetland species, *Phragmites australis* and *Glyceria maxima*. New Phytol 173(2):264–278

Sousa FC, Melo CT, Monteiro AP, Lima VT, Gutierrez SJ, Pereira BA, Barbosa-Filfo JM, Vasconselos SM, Viana GS (2004) Antianxiety and antidepressant effects of riparin III from *Aniba riparia* (Nees) Mez (Lauraceae) in mice. Pharmacol Biochem Behav 78(1):27–33

Souza MC (2006) Variações morfológicas, moleculares e fitoquímicas do complexo *Geonoma maxima* (Poit.) Kunth (Arecaceae) na Amazônia: elucidação de um problema taxonômico. Ph.D. thesis, CNPq, INPA/UFAM, Manaus

Sprent JI (1987) The ecology of the nitrogen cycle. Cambridge University Press, Cambridge

Sprent JI (1995) Legume trees and shrubs in the tropics: N_2 fixation in perspective. Soil Biol Biochem 27(4/5):401–407

Sprent JI (1999) Nitrogen fixation and growth of non-crop legume species in diverse environments. Perspect Plant Ecol Evolut System 2(2):149–162

Spruce R (1908) Notes of a botanist on the Amazon and Andes. MacMillan, London

Sprugel DG, Benecke U (1991) Measuring woody-tissue respiration and photosynthesis. In: Lassoie JP, Hinckley TM (eds) Techniques and approaches in forest tree ecophysiology, vol 1. CRC Press, Boston, pp 329–355

Stadtler EWC (2007) Estimativas de biomassa lenhosa, estoque e seqüestro de carbono acima do solo ao longo do gradiente de inundação em uma floresta de igapó alagada por água preta na Amazônia Central. M.Sc. thesis, INPA/UFAM, Manaus, Brazil

Stahle DW, Mushove PT, Cleaveland MK, Roig F, Haynes GA (1999) Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. Forest Ecol Manag 124:217–229

Stark N, Spratt M (1977) Root biomass and nutrient storage in rain forest Oxisols near San Carlos de Rio Negro. Trop Ecol 18:1–9

HO'R S (1987) Aggravation of floods in the Amazon river as a consequence of deforestation? Geografiska Annaler 69A:201–219

Sternberg HO'R (1998) A água e o homem na várzea do Careiro, 2 edn. Museu Paraense Emílio Goeldi, Belém

Stevens KJ, Larry Peterson R, Reader RJ (2002) The aerenchymatous phellem of *Lythrum salicaria* (L.): a pathway for gas transport and its role in flood tolerance. Ann Bot 89:621–625

Steyermark JA (1982) Relationships of some Venezuelan refuges with lowland tropical Floras. In: Prance GT (ed) Biological diversification in the tropics. Columbia University Press, New York, pp 182–220

Stiles FG (1975) Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. Ecology 56:285–301

Stiles FG (1977) Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. Science 198:1170–1178

Stoner KE, Riba-Hernández P, Vulinec K, Lambert JE (2007a) The role of mammals in creating and modifying seedshadows in tropical forests and some possible consequences of their elimination. Biotropica 39:316–327

Stoner KE, Vulinec K, Wright SJ, Peres CA (2007b) Hunting and plant community dynamics in tropical forests: a synthesis and future directions. Biotropica 39:316–327

Suffredini IB, Varella D, De Oliveira AA, Younes RN (2002) In-vitro anti-HIV and antitumor evaluation of Amazonian plants belonging to the Apocynaceae family. Phytomedicine 9:175

Surgik ACS (2005) Estrudo Jurídico para a várzea Amazônica. In: Benfatti JH, Surgik ACS, Treccani GD, McGrath DG, da Gama ASP (eds) Aquestão fundiária e o maejo dos recursos naturais da várzea: análise para a elaboração de novos modelos jurídicos. ProVárzea/IBAMA, Manaus, Brazil, pp 15–32

Sutton SI, Whitmore TC, Chadwick AC (1983) Tropical rain forest ecology and management, Blackwell Scientific, Oxford, pp 59–75

Swaine MD, Beer T (1977) Explosive seed dispersal in *Hura crepitans* L. (Euphorbiaceae). New Phytol 78:695–708

Swaine MD, Whitmore TC (1988) On the definition of ecological species groups in tropical rain forests. Vegetatio 75:81–86

Swofford DL (1998) *PAUP** – Phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts

Sylvester-Bradley R, de Oliveira LA, de Podestá Filho JA, John TVS (1980) Nodulation of legumes, nitrogenase activity of roots and occurrence of nitrogen-fixing *Azospirillium* spp. in representative soils of central Amazonia. Agro-Ecosystems 6:249–266

Szaniszlo PJ, Powell PE, Reid CPP, Cline GR (1981) Production of hydroxymate siderophore iron chelators by ectomycorrhizal fungi. Mycologica 73:1158–1178

Taiz L, Zeiger E (2004) Fisiologia vegetal. Trad. Eliane Romanato Santarém 3a. ed.– Porto Alegre. Artmed. p 719

Takeuchi M (1962) The structure of the Amazonian vegetation. 6. Igapó. J Fac Sci Univ Tokyo Sect Bot 3:297–304

Talbot RW, Andreae MO, Berresheim H, Jacob DJ, Beecher KM (1990) Sources and sinks of formic, acetic, and pyruvic acids over central Amazonia.2. Wet Season. J Geophys Res Atmos 95:16799–16811

Tallak Nilsen E, Muller WH (1981) Phenology of the drought-deciduous shrub *Lotus scoparius*: climatic controls and adaptive significance. Ecolog Monograph 51:323–341

Tansley AG (1929) Succession: the concept and its values. Proceedings of the 4th international congress plant science, Ithaca, 1926, pp 677–686

Ter Steege H (2000) Plant diversity in Guyana. With recommendation for a protected areas strategy. Tropenbos Series 18, Tropenbos Foundation, Wageningen

Ter Steege H, Sabatier D, Castellanos H, Van Andel T, Duivenvoorden J, de Oliveira AA, Ek R, Lilwah R, Maas P, Mori S (2000) An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana shield. J Trop Ecol 16:801–828

Ter Steege H, Pitman N, Sabatier D, Castellanos H, Van der Hout P, Daly DC, Silveira M, Phillips OL, Vasquez R, Van Andel T, Duivenvoorden J, de Oliveira AA, Ek R, Lilwah R, Thomas R, Van Essen J, Baider C, Maas P, Mori S, Terborgh J, Núñez PV, Mogollón H, Morawetz W (2003) A spatial model of tree α-diversity and -density for the Amazon Region. Biodivers Conserv 12(11):2255–2277

Ter Steege H, Pitman N, Phillips OL, Chave J, Sabatier D, Duque A, Molino JF, Prévost MF, Spichiger R, Castellanos H, Hildebrand P, Vásquez R (2006) Continental scale patterns of canopy tree composition and function across Amazonia. Nature 443, doi 10.1038/nature05134

Terborgh J (1990) Seed and fruit dispersal – commentary. In: Bawa KS, Hadley M (eds) Reproductive ecology of tropical forest plants. Man and the biosphere series 7:181–190

Terborgh J, Petren K (1991) Development of habitat structure through succession in an Amazonian floodplain forest. In: Bell SS (ed) Habitat Structure. Chapman and Hall, London, pp 28–46

Terborgh J, Flores CN, Mueller P, Davenport L (1997) Estimating the ages of successional stands of tropical trees from growth increments. J Trop Ecol 14:833–856

Terborgh J, Andresen E (1998) The composition of Amazonian forests: patterns at local and regional scales. J Trop Ecol 14:645–664

Therrell MD, Stahle DW, Diaz JV, Oviedo EH, Cleaveland MK (2006) Tree-ring reconstructed maize yield in central Mexico: 1474–2001. Climat Change 74:493–504

Thielen-Klinge A (1997) Rolle der biologischen N_2-Fixierung von Baumleguminosen im östlichen Amazonasgebiet, Brasilien – Anwendung der ^{15}N natural abundance Methode. Ph.D. thesis, University of Göttingen

Thienemann A (1918) Lebensgemeinschaft und Lebensraum. Naturwiss Wochenschrift NF 17:282–303

Thomaz SM, Agostinho AA, Hahn NS (2004) The upper Paraná River and its floodplain: physical aspects, ecology and conservation. Blackhuys Publishers, Leiden

Thompson AM (1992) The oxidizing capacity of the earth's atmosphere – probable past and future changes. Science 256:1157–1165

Thomson CJ, Armstrong W, Waters I, Greenway H (1990) Aerenchyma formation and associated oxygen movement in seminal and nodal roots of wheat. Plant Cell Environ 13:395–403

Tian H, Melillo JM, Kicklighter DW, McGuire AD, Helfrich JVK, Moore B III, Vörösmarty CJ (1998) Effect of interannual climate variability on carbon storage in Amazonian ecosystems. Nature 396:664–667

Timmermann A, Oberhuber J, Bacher A, Esch M, Latif M, Roeckner E (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature 398:694–697

Toivonen T, Mäki S, Kalliola R (2007) The riverscape of Western Amazonia – a quantitative approach to the fluvial biogeography of the region. J Biogeogr 34:1374–1387

Toledo FF, Marcos Filho J (1977) Manual de Sementes – tecnologia da produção. Agronômica Ceres, São Paulo, p 244

Topa MA, McLeod KW (1986) Aerenchyma and lenticel formation in pine seedlings: a possible avoidance mechanism to anaerobic growth conditions. Physiol Plant 68:540–550

Torres-Santos EC, Lopes D, Oliveira RR, Carauta JP, Falcão CA, Kaplan MA, Rossi-Bergmann B (2004) Antileishmanial activity of isolated triterpenoids from *Pourouma guianensis*. Phytomedicine 11(2–3):114–120

Trappe JM, Fogel R (1977) Ecosystematic functions of mykorrhizae. In: Marschall JM (ed) The belowground ecosystem: a synthesis of plant-ssociated processes. Range Science Department Science Ser 26, Colorado State University, Fort Collins, Colorado, USA, pp 205–214

Treccani GD (2005) Identificação e análise dos diferentes tipos de apropriação da terra e suas implicações para o uso dos recursos naturais renováveis da várzea Amazônica, no imóvel rural, na área de Gurupá. In: Benfatti JH, Surgik ACS, Treccani GD, McGrath DG, da Gama ASP (eds) Aquestão fundiária e o maejo dos recursos naturais da várzea: análise para a elaboração de novos modelos jurídicos. ProVárzea/IBAMA, Manaus, Brazil, pp 55–74

Trenberth KE (2005) Uncertainty in hurricanes and global warming. Science 308:1753–1754

Tsai SM, Nodari RO, Moon DH, Camargo LEA, Vencovsky R, Gepts P (1998) QTL mapping for nodule number and common bacterial blight in *Phaseolus vulgaris* L. Plant Soil 204(1):135–145

Tuomisto H, Ruokolainen K, Salo J (1992) Lago Amazonas: fact or fancy? Acta Amazonica 22(3):353–361

Tuomisto H, Ruokolainen K, Kalliola R, Linna A, Danjoy W, Rodriguez Z (1995) Dissecting Amazonian biodiversity. Science 269:63–66

Turner IM (1994) Sclerophylly: primarily protective? Function Ecol 8:669–675

U.S. Soil Taxonomy (1990) Keys to soil taxonomy by soil survey staff. Agency for international development United States department of agriculture soil management support services. SMSS Technical Monograph No 19, 4th edn. Cornell University

Uhl C, Baretto P, Veríssimo A, Barros AC, Amaral P, Vidal E, Souza C Jr (1998) Uma abordagem integrada de pesquisa sobre o manejo dos recursos florestais na Amazônia brasileira. In: Gascon C, Moutinho P (eds) Floresta Amazônica: Dinâmica, Regeneração e Manejo. MCT/INPA, Manaus, Brazil, pp 313–331

Val AL, Rolim PR, Rebelo H (2000) Situação atual da aquacultura na região Norte. In: Valenti WC, Poli RC, Pereira JA, Borghetti JR (eds) Aquacultura no Brasil: bases para um desenvolvimento sustentável. CNPq, Ministério da Ciência e Tecnologia, Brasília, pp 246–266

Valencia R, Balslev H, Paz y Mino CG (1994) High tree alpha diversity in Amazonian Ecuador. Biodivers Conserv 3:21–28

Valle D, Schulze M, Vidal E, Grogan J, Sales M (2006) Identifying bias in stand-level growth and yield estimations: a case study in eastern Brazilian Amazonia. Forest Ecol Manag 236:127–135

Van der Hammen T (1974) The Pleistocene changes of vegetation and climate in tropical South America. J Biogeogr 1:3–26

Van der Hammen T, Wymstra TA (1964) A palynological study on the tertiary and upper cretaceous of British Guyana. Leidse Geologische Mededelingen 30:183–241

Van der Hammen T, Garcia M (1966) The paleocene pollen flora of Colombia. Leidse Geologische Mededelingen 35:105–166

Van der Hammen T, Hooghiemstra H (2000) Neogene and quaternary history of vegetation, climate, and plant diversity in Amazonia. Quatern Sci Rev 19:725–742

Van Gardingen PR, Valle D, Thompson I (2006) Evaluation of yield regulation options for primary forest in Tapajós National Forest, Brazil. Forest Ecol Manag 231:184–195

van Schaik CP (1986) Phenological changes in a Sumatran rain forest. J Trop Ecol 2:327–347

van Schaik CP, Terborgh JW, Wright SJ (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. Ann Rev Ecol System 24:353–377

Vanclay JK (1994) Modelling forest growth and yield: applications to mixed tropical forests. CAB International, Wallingford, UK

Vargas R, Allen MF, Allen EB (2008) Biomass and carbon accumulation in a fire chronosequence of a seasonally dry tropical. Global Change Biol 14:109–124

Veríssimo A, Barreto BP, Mattos M, Tarifa R, Uhl C (1992) Logging impacts and prospects for sustainable management in an old Amazonian frontier: the case of Paragominas. Forest Ecol Manag 55:169–199

Veríssimo A, Barreto BP, Tarifa R, Uhl C (1995) Extraction of a high-value natural resource in Amazonia: the case of mahogany. Forest Ecol Manage 72:39–60

Veríssimo J (1895) A pesca na Amazônia. Livraria Clássica de Alves, Rio de Janeiro, 206 pp

Viana JP, Damasceno JMB, Castello L (2003) Desarrollo del manejo pesquero comunitario en la Reserva de Mamirauá, Amazonas, Brasil. In: Campos-Rozo C, Ulloa A (eds) Fauna Socializada: tendencias en el manejo partecipativo de la fauna en America Latina. Fundación Natura MacArthur Foundation, Instituto Colombiano de Antropología e Historia, Bogtá, Colombia, pp 335–351

Viana JP, Damasceno JM, Castello L, Crampton W (2004) Economic incentives for sustainable community management of fishery resources in the Mamirauá Sustainable Development Reserve, Amazonas, Brazil. In: Silvius KM, Bodmer RE, Fragoso JM (eds) People in nature: wildlife conservation in South and Central America. Columbia University Press, New York, pp 139–154

Viana JP, Castello L, Damasceno JM, Amaral ESR, Estupiñan GMB, Arantes C, Batista GS, Garcez DS, Barbosa S (2007) Manejo comunitário do pirarucu *Arapaima gigas* na Reserva de Desenvolvimento Sustentável Mamirauá, Amazonas, Brasil. In: Prates APL, Blanc D (eds) Áreas aquáticas protegidas como instrumento de gestão pesqueira. Série Áreas Protegidas do Brasil. N.4. MMA-SBF-NZCM. Brasília, pp 239–261

Vidal E, Johns J, Gerwing JJ, Barreto P, Uhl C (1997) Vine management for reduced-impact logging in eastern Amazonia. Forest Ecol Manag 98:105–114

Vidal E, Viana VM, Batista JLF (2002) Crescimento de floresta tropical três anos após colheita de madeira com e sem manejo florestal na Amazônia oriental. Scientia forestalis 61:133–143

Vieira R, dos S (2000) Legislation and the use of Amazonian floodplains. In: Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds) The Central Amazon floodplain: actual use and options for a sustainable management. Backhuys Publishers bV, Leiden, The Netherlands, pp 505–533

Viera S, Trumbore S, Camargo PB, Selhorst D, Chambers JQ, Higuchi N, Martinelli LA (2005) Slow growth rate of Amazonian trees: consequences for carbon cycling. PNAS 102:18502–18507

Vinuesa P, Rademaker JLW, de Bruijn FJ, Werner D (1998) Genotypic characterisation of *Bradyrhizobium* strains nodulating endemic woody legumes of the Canary Islands by PCR-restriction fragment length polymorphism analyses of genes encoding 16S rRNA (16S rDNA) and 16S-23S rDNA intergenic spacers, repetitive extragenic palindromic PCR genomic fingerprinting and partial 16S rDNA sequencing. Appl Environ Microbiol 64(6):2096–2104

Visser EJW, Colmer TD, Blom CWPM, Voesenek LACJ (2000) Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma. Plant Cell Environ 23:1237–1245

Visser EJW, Voesenek LACJ (2004) Acclimation to soil flooding – sensing and signal-tranduction. Plant Soil 254:197–214

Vitousek PM (1982) Nutrient cycling and nutrient use efficiency. Am Nat 119:553–572

Vitousek PM (1984) Litterfall, nutrient cycling and nutrient limitation in tropical forests. Ecology 65(1):285–298

Voesenek LACJ, van der Sman AJM, Harren FJM, Blom CWPM (1992) An amalgamation between hormone physiology and plant ecology: a review on flooding resistance and ethylene. J Plant Growth Regulat 11(3):171–188

Voesenek LACJ, Banga M, Rijnders JGHM, Visser EJW, Blom CWPM (1996) Hormone sensitivity and plant adaptations to flooding. Folia Geobotanica 31(1):47–56

Voesenek LACJ, Benschop JJ, Bou J et al (2003) Interactions between plant hormones regulate submergence-induced shoot elongation in the flooding-tolerant dicot *Rumex palustris*. Ann Bot 91:205–211

Vogt KA, Grier CC, Gower ST, Sprugel DG, Vogt DJ (1986) Overestimation of net root production: a real or imaginary problem? Ecol 67(2):577–579

Vörösmarty CJ, Green P, Salisbury J, Lammers RB (2000) Global water resources: vulnerability from climate change and population growth. Science 289:284–288

Vuilleumier BS (1971) Pleistocene changes in the fauna and flora of South America. Science 1973:771–779

Wagenführ R (1989) Anatomie des Holzes. 4. neubearbeitete Auflage, VEB Fachbuchverlag Leipzig

Waldhoff D (1991) Morphologie, Nährwert und Bioelementgehalte hydrochor und zoochor verbreiteter Früchte und Samen aus amazonischen Überschwemmungswäldern bei Manaus. Unpublished Diploma thesis, University Kiel

Waldhoff D (1994) Analyse von Früchten aus den Überschemmungswäldern Zentralamazoniens und dem Pantanal Matogrossense in Hinsicht auf ihren Wert als Nahrung für kommerziell zu nutzende Fischarten. Unpublished Ph.D. thesis, University Kiel

Waldhoff D (2003) Leaf structure in trees of Central Amazonian floodplain forests (Brazil). Amazoniana 17:451–469

Waldhoff D, Furch B (1998) Effect of waterlogging and flooding on some abundant tree species of Central Amazonia examined under defined conditions in climatic chambers. Verhandlungen des Internationalen Vereins Limnologie 26:1886–1871

Waldhoff D, Furch B (1999) Chemical composition of fruits and seeds from floodplain biotopes of the Pantanal do Mato Grosso near Cuiabá, Brazil, in comparison to those from similar ones of Central Amazonia. Convergence 1:27–41

Waldhoff D, Furch B (2002) Leaf morphology and anatomy in eleven tree species from Central Amazonian floodplains (Brazil). Amazoniana 17:79–94

Waldhoff D, Saint-Paul U, Furch B (1996) Value of fruits and seeds from the floodplain forests of Central Amazonia as food resource for fish. Ecotropica 2:143–156

Waldhoff D, Junk WJ, Furch B (1998) Responses of three Central Amazonian tree species to drought and flooding under controlled conditions. Int J Ecol Environ 24:237–252

Waldhoff D, Junk WJ, Furch B (2000) Comparative measurements of growth and chlorophyll *a* fluorescence parameters of *Nectandra amazonum* under different environmental conditions in climatized chambers. Verh Intern Verein Limnol 27:2052–2056

Waldhoff D, Furch B, Junk WJ (2002) Fluorescence parameters, chlorophyll concentration, and anatomical features as indicators for flood adaptation of an abundant tree species in Central Amazonia: *Symmeria paniculata*. Environ Experimen Bot 48(3):225–235

Waldhoff D, Parolin P (2010) Morphology and anatomy of leafs. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

SBv W, Kuhn KM, Gworek JR (2005) Two-phase seed dispersal: linking the effects of frugivorous birds and seed-caching rodents. Oecologia 145:282–287

Walter H, Breckle SW (1984) Spezielle Oekologie der tropischen und subtropischen Zonen, Ökologie der Erde, Vol 2 Fischer, Stuttgart

Wand SJE, Midgley GF, Jones MH, Curtis PS (1999) Responses of wild C_4 and C_3 grass (Poaceae) species to elevated atmospheric CO2 concentration: a met analytic test for current theories and perceptions. Global Change Biol 5:723–741

Wang Y, Filoso S, Hess LL, Melack JM (1995) Understanding the radar backscattering from flooded and nonflooded Amazonian forests: results from canopy modeling. Remote Sens Environ 54:324–332

Wantzen KM (2003) Cerrado streams – characteristics of a threatened freshwater ecosystem type on the tertiary shields of Central South America. Amazoniana 17(3/4):481–502

Wantzen KM, Jule C, Tockner K, Junk WJ (2007) Riparian wetlands of tropical streams.In: Dudgeon D, Cressa C (eds) Tropical stream ecology. Elsevier, London

Waring RH, Schlesinger WH (1985) Forest ecosystems: concepts and management. Academic Press, Orlando

Wassmann R, Martius C (1997) Methane emissions from the Amazon floodplain. In: Junk WJ (ed) The Central Amazon floodplains. Ecology of a pulsing system. Springer, Berlin/Heidelberg/New York, pp 137–143

Way H, Chapman S, McIntyre L, Casu R, Xue GP, Manners J, Shorter R (2005) Identification of differentially expressed genes in wheat undergoing gradual water deficit stress using a subtractive hybridisation approach. Plant Sci 168:661–670

Weibel EW (1979) Stereological methods, vol 1: practical methods for biological morphometry, p 415. Academic Press, New York

Weischet W (1977) Die ökologische Benachteiligung der Tropen. Stuttgart

Weising K, Gardner RC (1999) A set of conserved PCR primers for the analysis of simple sequence repeat polymorphisms in chloroplast genomes of dicotyledonous angiosperms. Genome 42:9–19

Wenk EH, Dawson TE (2007) Interspecific differences in seed germination, establishment, and early growth in relation to preferred soil type in an alpine community. Arct Antarct Alpine Res 39:165–176

Wesselingh FP, Salo JA (2006) Miocene perspective on the evolution of the Amazonian biota. Scripta Geol 133:439–458

Whetton P, Rutherfurd I (1994) Historical ENSO teleconnection in the eastern hemisphere. Climat Change 28:221–253

White A, Cannell MGR, Friend AD (1999) Climate change impacts on ecosystems in the terrestrial carbon sink: new assessment. Global Environ Chang 9:S21–S30

Whiteman PC, Seitlheko M, Siregar ME, Chudasama AK, Javier RR (1984) Short-term flooding tolerance of seventeen commercial tropical pasture legumes. Trop Grasslands 18(2):91–96

Whitmore TC (1984) Tropical rainforests of the far east, 2nd edn. Clarendon Press, Oxford

Whitmore TC (1989) Canopy gaps and the two major groups of forest trees. Ecology 70:536–537

Whitmore TC (1990) An introduction to tropical rain forests. Oxford, Claredon Press, p 226

Whitmore TC (1993) Tropische Regenwälder: Eine Einführung. Spektrum Akad. Springer, Heidelberg/Berlin/New York

Whitmore TC (1998) An introduction to tropical rain forests, 2nd edn. Oxford University Press, Oxford

Whittaker RH (1953) A consideration of climax theory: the climax as a population and pattern. Ecol Monogr 23:41–78

Wiemann MC, Williamson GB (1989) Wood specific gravity gradients in tropical dry and montane forest trees. Am J Bot 76:924–928

Wiengweera A, Greenway H, Thomson CJ (1997) The use of agar nutrient solution to simulate lack of convection in waterlogged soils. Ann Bot 80:115–123

Wilkinson HP (1979) The plant surface. In: Metcalfe CR, L Chalk (eds) Systematic anatomy of leaf and stem, pp 97–165. Clarendon Press, Oxford

Williams E, Antonia AD, Antonia VD, Almeida JD, Suarez F, Liebmann B, Malhado ACM (2005) The drought of the century in the Amazon basin: an analysis of the regional variation of rainfall in South America in 1926. Acta Amazonica 35:231–238

Williams WM, Hoh CH, Lenz F, Broughton WJ (1988) Rhizobia in tropical legumes: environmental factors and the reduction of nitrogen. Soil Biol B 20:667–675

Williams-Linera G (1997) Phenology of deciduous and broad leaf evergreen tree species in a Mexican tropical lower montane forest. Global Ecol Biogeogr Lett 6:115–127

Williamson GB, Costa F (2000) Dispersal of amazonian trees: hydrochory in *Pentaclethra macroloba*. Biotropica 32:548–552

Williamson GB, Costa F, Minte Vera CV (1999a) Dispersal of Amazonian trees: hydrochory in *Swartzia polyphylla*. Biotropica 31:460–465

Williamson GB, Van Eldik T, Delamônica P, Laurance WF (1999b) How many millenarians in Amazonia: sizing the ages of large trees. Trends Plant Sci 4(10):386–387

Wilson MD, Bates PD, Alsdorf D, Forsberg BR, Horritt M, Melack JM, Frappart F, Famglietti JS (2007) Modeling large-scale inundation of Amazonian seasonally flooded wetlands. Geophys Res Let 34:L15404. doi:10.1029/2007GL030156

Wingler A, von Schaewen A, Leegood RC, Lea PJ, Quick WP (1998) Regulation of senescence by citokinin, sugars and light. Plant Physiol 116:329–335

Wittmann F (1997) Die Várzea-Wälder Zentralamazoniens – Phänologische Untersuchungen ausgewählter Baumarten zur Reaktion auf den annuellen Flutungsstreß. Master thesis, Geographisches Institut Universität Mannheim, p 89

Wittmann F (2001) Artenverbreitung und Bestandesstruktur in amazonischen Várzea-Wäldern und Möglichkeiten der Erfassung von Waldtypen mittels fernerkundlichen Methoden. Ph.D. thesis, Universität Mannheim, Fachbereich Geographie

Wittmann F, Anhuf D, Junk WJ (2002a) Detection of different forest types in Central Amazonian Várzea by remote sensing techniques – preliminary results. In: Lieberei R, Bianchi H-K, Boehm V, Reisdorff C (eds) Neotropical ecosystems. Proceedings of the German-Brazilian Workshop, Hamburg 2000, GKSS-Geesthacht, Germany, pp 607–661

Wittmann F, Anhuf D, Junk WJ (2002b) Tree species distribution and community structure of central Amazonian várzea forests by remote-sensing techniques. J Trop Ecol 18: 805–820

Wittmann F, Junk WJ (2003) Sapling communities in Amazonian white-water forests. J Biogeogr 30:1533–1544

Wittmann F, Junk WJ, Piedade MTF (2004) The várzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. Forest Ecol Management 196:199–212

Wittmann F, Oliveira Wittmann A (2010) Use of Amazonian floodplain trees. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Wittmann F, Parolin P (1999) Phenology of six tree species from central Amazonian várzea. Ecotropica 5(1):51–57

Wittmann F, Parolin P (2005) Aboveground roots in Amazonian white-water forests. Biotropica 37:609–619

Wittmann F, Schöngart J, Montero JC, Motzer M, Junk WJ, Piedade MTF, Queiroz HL, Worbes M (2006) Tree species composition and diversity gradients in white-water forests across the Amazon Basin. J Biogeogr 33:1334–1347

Wittmann F, Schöngart J, Parolin P, Worbes M, Piedade MTF, Junk WJ (2006b) Wood specific gravity of trees in Amazonian white-water forests in relation to flooding. IAWA J 27(3):255–266

Wittmann F, Schöngart J, Queiroz HL, Oliveira Wittmann A, Conserva AS, Piedade MTF, Kesselmeier J, Junk WJ (2009)The Amazon floodplain demonstration site: sustainable timber production and management of Central Amazonian white-water floodplains. Ecohydrology and Hydrobiology: doi 10.2478/v10104-009-0038-4

Wittmann F, Schöngart J, Junk WJ (2010) Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forests. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Wittmann F, Schöngart J, Brito JM, Oliveira Wittmann A, Parolin P, Piedade MTF, Junk WJ and Guillaumet J-L (in press) Manual of tree species in central Amazonian white-water floodplains: Taxonomy, Ecology, and Use. Instituto Nacional de Pesquisas da Amazonia - INPA, Universidade Estadual do Amazonas - UEA, Instituto de Desenvolvimento Sustentável Mamirauá - ISDM. Editora Valer, Manaus, Rio de Janeiro, Brazil

Witty JF, Skøt L, Revsbech NP (1987) Direct evidence for changes in the resistance if legume root nodules to O_2 diffusion. J Exp Bot 38(192):1129–1140

Worbes M (1983) Vegetationskundliche Untersuchungen zweier Überschwemmungswälder in Zentralamazonien – vorläufige Ergebnisse. Amazoniana 8(1):47–66

Worbes M (1984) Periodische Zuwachszonen an Bäumen zentralamazonischer Überschwemmungswälder. Naturwissenschaften 71:157–158

Worbes M (1985) Structural and other adaptations to longterm flooding by trees in Central Amazonia. Amazoniana 9:459–484

Worbes M (1986) Lebensbedingungen und Holzwachstum in zentralamazonischen Überschwemmungswäldern. Erich Goltze, Göttingen. Scripta Geobotanica 17:1–112

Worbes M (1988) Variety in structure of annual growth zones in Tabebuia barbata (E. Mey) Sandw., Bignoniaceae, a tropical tree species from Central Amazonian inundation forests. Dendrochronologia 6:71–89

Worbes M (1989) Growth rings, increment and age of tree in inundation forest, savannas and a mountain forest in the Neotropics. IAWA Bull 10(2):109–122

Worbes M (1992) Occurrence of seasonal climate and tree-ring research in the tropics. Lundqua Report 34:338–342

Worbes M (1994) Grundlagen und Anwendungen der Jahresringforschung in den Tropen. Universität of Hamburg, Habilitationsschrift

Worbes M (1995) How to measure growth dynamics in tropical trees – a review. IAWA J 16:337–351

Worbes M (1996) Rhythmisches Wachstum und anatomisch-morphologische Anpassungen an Lebensstrategien von Bäumen in zentralamazonischen Überschwemmungswäldern. Mitt Dtsch Dendrol Ges 82:155–172

Worbes M (1997) The forest ecosystem of the floodplains. In: Junk WJ (ed) The central Amazon floodplain: ecology of a pulsating system. Ecolog Stud 126:223–265. Springer, Berlin/Heidelberg/New York

Worbes M (1999) Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. J Ecol 87:391–403

Worbes M (2002) One hundred years of tree ring research in the tropics – a brief history and an outlook to future challenges. Dendrochronologia 20(1–2):217–231

Worbes M, Junk WJ (1989) Dating tropical trees by Means of ^{14}C from Bomb tests. Ecology 70(2):503–507

Worbes M, Klinge H, Revilla JD, Martius C (1992) On the dynamics, floristic subdivision and geographical distribution of várzea forests in Central Amazonia. J Vegetat Sci 3:553–564

Worbes M, Klosa D, Lewark S (1995) Rohdichtestruktur von Jahresringen tropischer Hölzer aus zentralamazonischen Überschwemmungswäldern. Holz Roh Werkst 53:63–67

Worbes M, Junk WJ (1999) How old are tropical trees? The persistence of a myth. IAWA J 20(3):255–260

Worbes M, Piedade MTF, Schöngart J (2001) Holzwirtschaft im Mamirauá-Projekt zur nachhaltigen Entwicklung einer Region im Überschwemmungsbereich des Amazonas. Forstarchiv 72: 188–200

Worbes M, Staschel R, Roloff A, Junk WJ (2003) Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. Forest Ecol Manag 173:105–123

Worbes M, Fichtler E (2010) Wood anatomy and tree-ring structure and their importance for tropical dendrochronology. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Berlin/Heidelberg/New York

Wright SJ (1991) Seasonal drought and the phenology of understory shrubs in a tropical moist forest. Ecology 72:1643–1657

Wright SJ, Cornejo FH (1990) Seasonal drought and leaf fall in a tropical forest. Ecology 71: 1165–1175

Wright SJ, van Schaik CP (1994) Light and the phenology of tropical trees. Am Nat 143:192–199

Wright SJ, Calderón O (1995) Phylogenetic patterns among tropical flowering phenologies. J Ecol 83:937–948

Wyatt-Smith J (1963) Manual of Malayan silviculture for inlnad forests, parts I–III. Malayan Forest Records no. 23, Forest Research Institute, Kepong

Wyatt-Smith J (1995) Manual of Malayan silviculture for inland forests, 2nd edn. Malayan Forest Record No. 23. Forest Research Institute Malaysia, Kuala Lumpur, Malaysia

Yao J (1970) Influence of growth rate on specific gravity and other selected properties of Loblolly Pine. Wood Sci Technol 4:163–175

Yoda K (1967) Comparative ecological studies on three main types of forest vegetation in Thailand. III. Community respiration. Nat Life SE Asia 5:83–148

Yoneyama T, Muraoka T, Murakami T, Boonkerd N (1993) Natural abundance of ^{15}N in tropical plants with emphasis on tree legumes. Plant Soil 153:295–304

Young JPW, Haukka KE (1996) Diversity and phylogeny of rhizobia. New Phytol 133:87–94

Zaerr JB (1983) Short-term flooding and net photosynthesis in seedlings of three conifers. Forest Sci 29(1):71–78

Zagt RJ, Werger MJA (1998) Community structure and demography of primary species in tropical rain forest. In: Newbery DM, Prins HHT, Brown N (eds) Dynamics of tropical communities. Blackwell Scientific, Cambridge, pp 193–220

Zeilhofer P (1996) Geoökologische Charakterisierung des nördlichen Pantanal von Mato Grosso, Brasilien, anhand multitemporaler Landsat Thematic Mapper-Daten. Dissertation, Herbert Utz Verlag, München

Zhang ZX, Zou XL, Tang WH, Zheng YL (2005) Revelation on early response and molecular mechanism of submergence tolerance in maize roots by microarray and suppression subtractive hybridization. Environ Experimen Bot 58(1/3):53–63

Ziburski A (1990) Ausbreitungs- und Reproduktionsbiologie einiger Baumarten der amazonischen Überschwemmungswälder. Unpublished Ph.D. thesis, University Hamburg

Ziburski A (1991) Dissemination, Keimung und Etablierung einiger Baumarten der Überschwemmungswälder Amazoniens. In: Rauh W (ed) Tropische und subtropische Pflanzenwelt. Akademie der Wissenschaften und der Literatur 77:1–96

Ziegler AM, Eshel G, McAllister Rees P, Rothfus TA, Rowley DB, Sunderlin D (2003) Tracing the tropics across land and sea: permian to present. Lethaia 36:227–254

Zimmermann HM, Hartmann K, Schreiber L, Steudle E (2000) Chemical composition of apoplastic transport barriers in relation to radial hydraulic conductivity of corn roots (*Zea mays* L.). Planta 210:302–311

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