Physiological and Anatomical Adaptations by Young Astrocaryum jauari Mart. (Arecaceae) in Periodically Inundated Biotopes of Central Amazonia

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ABSTRACT

Young plants of the palm, *Astrocaryum jauari*, are well-adapted anatomically and physiologically to hypoxic conditions. Annual inundation for as long as 300 days, at water temperatures of 28°C, produce neither leaf loss nor rotting of the roots. At a depth of 1.2 m beneath blackwaters, the leaves in the crowns of the plants show little decrease in the amount of chlorophyll. In contrast, submersion to an equal depth in whitewater produces a loss of chlorophyll. Photosynthetic oxygen production decreases to less than 30 percent of the terrestrial rate in plants submerged beneath blackwater, and to less than 10 percent in plants submerged in whitewater. Ethanol production compensates for temporary energy deficits. Respiration by the roots is greatly reduced but does not cease during inundation. Well-developed aerenchyma permits gas transport from the branches to the roots. A cylinder of stone cells and sclerenchyma fibers in the outer periphery of the primary bark prevents the collapse of the root aerenchyma due to reduced pressure within the roots and increasing external pressure as water depth rises.

Key words: *Amazonia; Astrocaryum; ethanol; flood plains; hypoxia; inundation; malate.*

IN VÁRZEA FORESTS AND IGAPÓ HABITATS (white and blackwater inundation forests) water levels may fluctuate as much as 15 m annually, creating stress on vegetation that is primarily terrestrial. The aquatic phase may be longer than the terrestrial phase. Blackwater conditions differ from the whitewater conditions by a higher light penetration, lower pH, and lower nutrient level. Adaptations by the plants to these different extreme conditions have seldom been investigated (Furch 1984). Hypoxia and insufficient illumination are the main stress factors for the plants of the understory and their epiphytes, both fully submerged during the aquatic phase. Furthermore, the availability of nutrients in the soil is greatly reduced due to the anoxia caused by inundation (Ponnamperuma 1977). The result is normally reduced growth, decomposition of chlorophyll

(Sena Gomes & Kozlowski 1988), and loss of the leaves (Kawase 1974). Thus, poorly adapted plants are subject to a high mortality rate after long inundation phases (Kozlowski 1984).

Among survivors of inundation, ethanol and lactate (Bertani *et al.* 1980) as well as alanine (Bertani & Brambilla 1982a) are often detected in the roots. These are the metabolites of anaerobic glucose metabolism that makes energy available to the plants. Furthermore, elevated concentrations of malate are often found in the plant tissues exposed to periods of oxygen shortages (Crawford 1971a, b; Keeley 1978; Bertani & Brambilla 1982b).

We hypothesed that *Astrocaryum jauari*, a common plant in both white and blackwater inundation forests, should have these metabolic adaptations to inundation stress. We also examined anatomy, respiration and photosynthesis rates, root carbohydrate content, the amount of soluble proteins in the leaves and roots, the chlorophyll content of the leaves, and the relative water content of the leaves and roots.
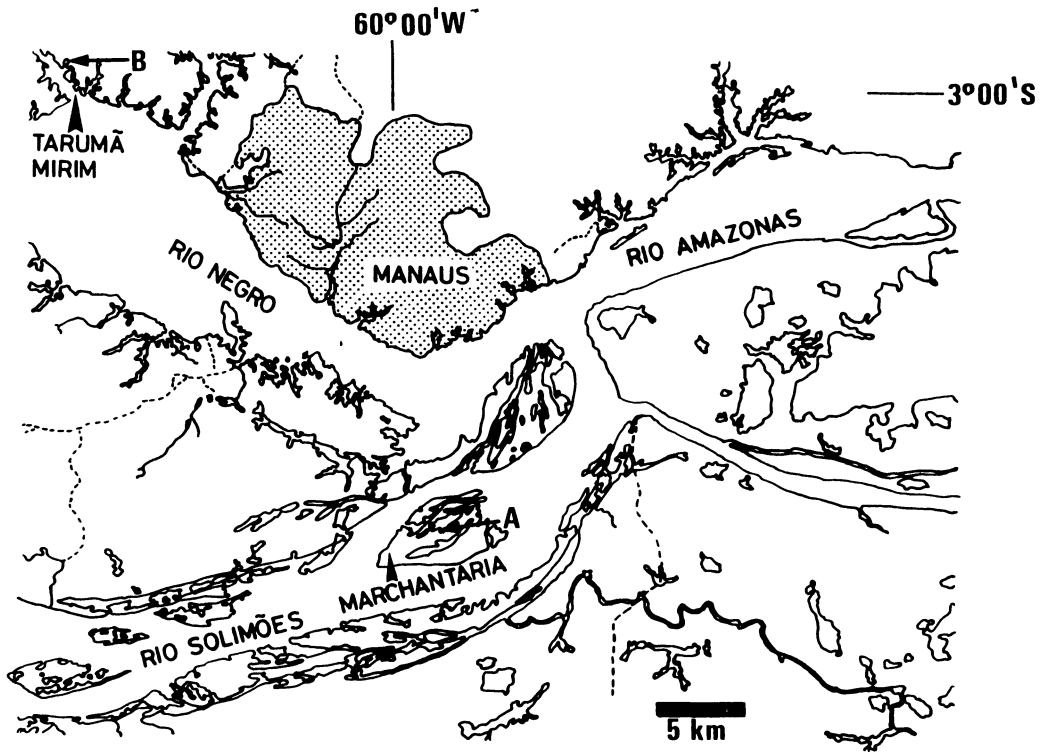
FIGURE 1.   Map of the region investigated showing locations of the white and blackwater flood plains in the watersheds of the Rio Solimões section of the Amazon and the Rio Negro, which join at Manaus, Brazil. (A) The várzea area (B) The igapó area.

METHODS

We selected two locations about 20 km from Manaus, Amazonia, one in the inundated várzea forest, located on the Ilha de Marchantaria (3°15'S, 59°58'W), and the other in the blackwater igapó (Prance 1979, Klinge 1983) along the shore of the creek Nova Inveja (3°2'S, 60°17'W), a tributary of the Taruma Mirim (Fig. 1). The inundation forests at both locations are secondary forests, which are subject to relatively little anthropogenic influence. Both locations are subject to an annual flood pulse of about 10 m in the surroundings of Manaus resulting from great changes in water volume carried by the Amazon river system.

Astrocaryum jauari, a palm in the subfamily Arecoideae, is widely distributed in the inundation forests and forms dominant stands on some of the islands in the Rio Negro (Goulding et al. 1988). The young palms are found densely clustered beneath the parent trees in the várzea. In the igapó, they are less densely clustered, presenting a rather evenly distributed occurrence. They are more abundant in the low-lying areas of the igapó.

The plant specimens from both the submerged and terrestrial sites gathered during 151 one-day excursions were cleaned in the field, then either shock frozen in liquid nitrogen and transported on dry ice for the determination of the metabolite content (transported on ice for the examinations of living material and the subsequent determination of dry weight); or fixed immediately for examination under the scanning electron microscope. In all physiological analyses, the entire root masses of 10 healthy, intact plants were pooled, and 3 random samples were taken from the material. The same 10 plants were used for the leaf samples. The youngest, fully developed leaf from each was taken, and the samples were obtained from the pooled material. To determine the water content as well as for the carbohydrate and alanine analyses, the material was freeze-dried to constant weight. The chlorophyll concentration in the fresh leaves was determined according to the method of Ziegler and Egle (1967),
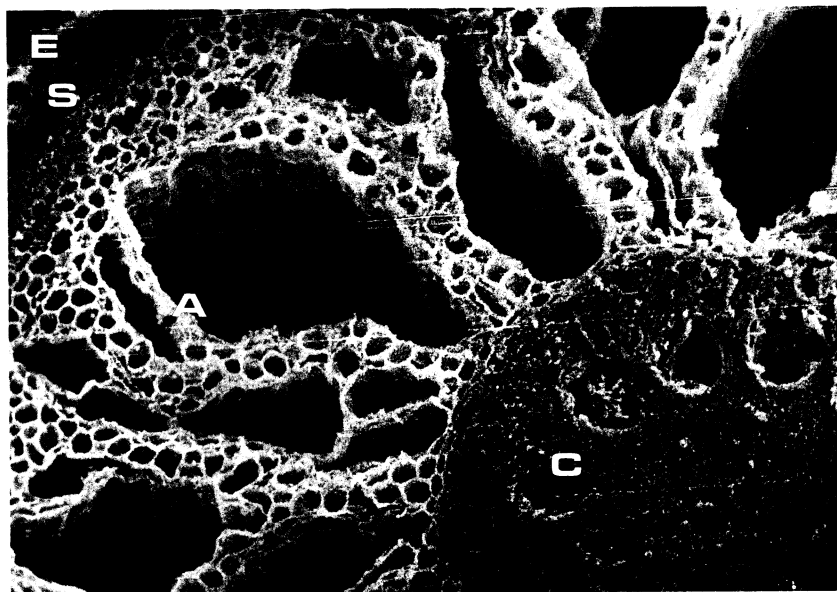
FIGURE 2.   Cross section through the aerenchyme of the roots of *Astrocaryum jauari*. Concentrically from the outside to the center are layers of epidermis and hypodermis (E), a ring of sclerenchyme (S), the aerenchyme (A), and the central cylinder (C); scale bar = 100 μm.

using 80 percent acetone for the extraction. The soluble protein fraction of the leaves and roots was determined using fresh material in 2 M tris-(hydroxymethyl) aminomethane with coomassie blue G250 (Bradford 1976). The quantitative carbohydrate analysis was conducted using the anthrone method described by Paech and Tracy (1955). The rate of net photosynthesis was calculated from the oxygen production according to the "Warburg-method" with light sources for each leaf disk in 0.08 M sodium bicarbonate buffer. The determination of the quantum flow density was conducted using an underwater sensor that was cosine corrected and functioned in the PAR band, 400 to 700 nm. To determine the respiration of the roots, a Warburg device was employed containing the following glucose solution: 0.25 M D-glucose, 0.002 M cysteine, 0.05 M tris-(hydroxymethyl) aminomethane, and 1 g gamma globulin per liter at pH 7.6. Ethanol, lactate, and malate were determined according to standard methods used in food analysis. Alanine analysis was performed using freeze-dried root material in a Type LC 6000 amino acid analyzer from the Biotronic Corporation. Mild extraction methods with water at 70°C for 5 min were used (Furch & Steinberg 1977). The fractionation columns and the program for the analyzer, employing single column stepwise elution, conform to the descriptions of Gabriel (1983).

RESULTS

The juvenile plants have shallow root systems which rarely penetrate deeper than 50 cm into the ground. Their annual biomass is low. As the flood waters rise, a rapid root growth is observed. It continues until the leaves become submerged, then all growth of the stems and roots ceases. After more than 300 days of submergence, the plants in the igapó still appear healthy, and leaves or roots displaying symptoms of necrosis are difficult to find. During the phase of receding water, the plants in the várzea begin to show the first signs of damage from the formation of hydrogen sulfide after about 200 days of submergence. Should the H_2S concentration continue to increase, the plants die in a short time. After a short period of emergence from the flood waters, new growth begins and only ceases after extremely dry, rainless weeks. Young plants contain aerenchyme tissue that may allow a continuous air exchange between the upper stems and the roots. The aerenchyme in the primary bark of the roots has a large lumen that occupies more than 1/3 of the total root diameter (Fig. 2). The firmness and resistance to pressure of the roots are provided by a cylinder of stone cells embedded in sclerenchyme fibers. The bilateral leaves are covered by a thick wax layer that protects against the flood waters. The stomata are located only on the underside of the

Várzea

respiration [µl O2/g fresh weight h]

Igapó

respiration [µl O2/g fresh weight h]
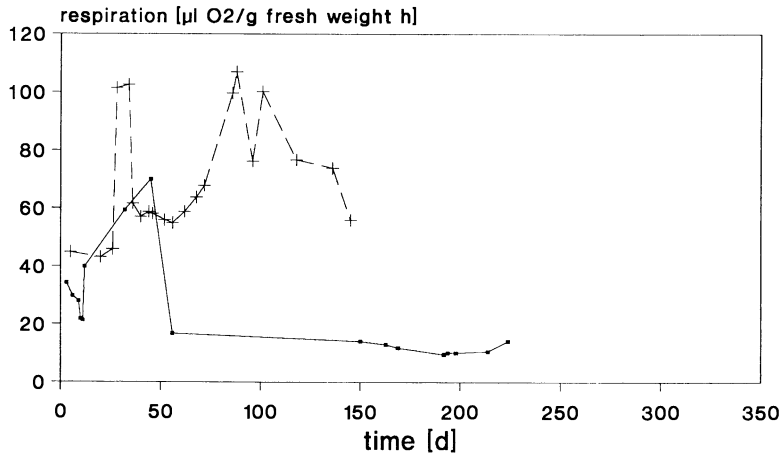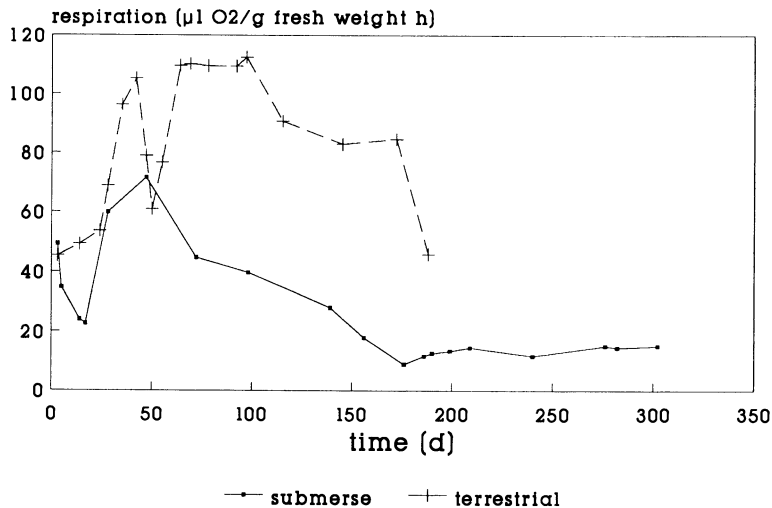
—•— submerse   —+— terrestrial

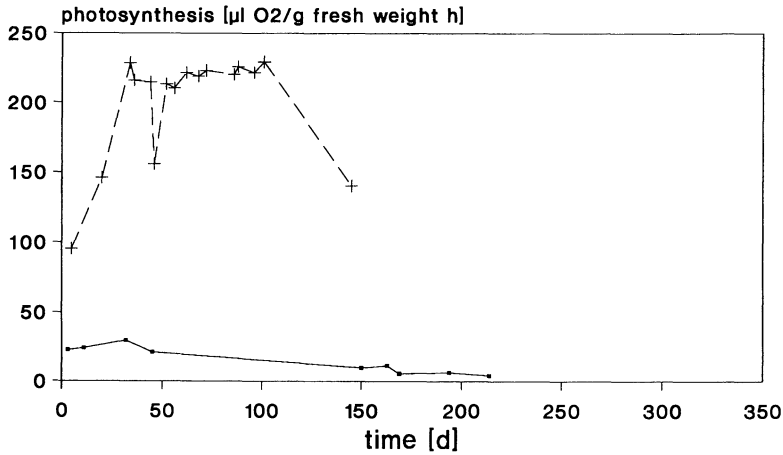FIGURE 3.   The rates of respiration during the inundation and the dry season in the várzea and the igapó.

leaves. Above the porus, there is a wax funnel that reduces evaporation during rainless periods and also keeps water from penetrating into the intercellular spaces while the leaves are submerged. Morphological changes induced by the flooding are not observed.

Oxygen consumption of the root tissue is reduced in submerged plants, but after more than 300 days of submergence, respiration is resumed after a short period of readjustment. Thus, it can be assumed that a functional capability is continuously maintained at all steps of the respiration pathway (Fig. 3).

At the beginning of the dry phase, the oxygen exchange begins a considerable initial increase. The drop in the exchange rate observed about 50 days after the plants had emerged was due to a shortage of water resulting from a lack of sufficient rainfall. The plants in the várzea show this sharp reduction more clearly (Fig. 3). In contrast, the decrease in the respiration rate at the end of the terrestrial phase is caused by the incipient drenching of the soil that occurs as the water level in the river rises again.

Photosynthesis follows a cycle similar to that of respiration (Fig. 4). Between the emergent and submerged phases, there is a clear change in the oxygen

Várzea

photosynthesis [µl O2/g fresh weight h]

time [d]

Igapó

photosynthesis (µl O2/g fresh weight h)

time (d)

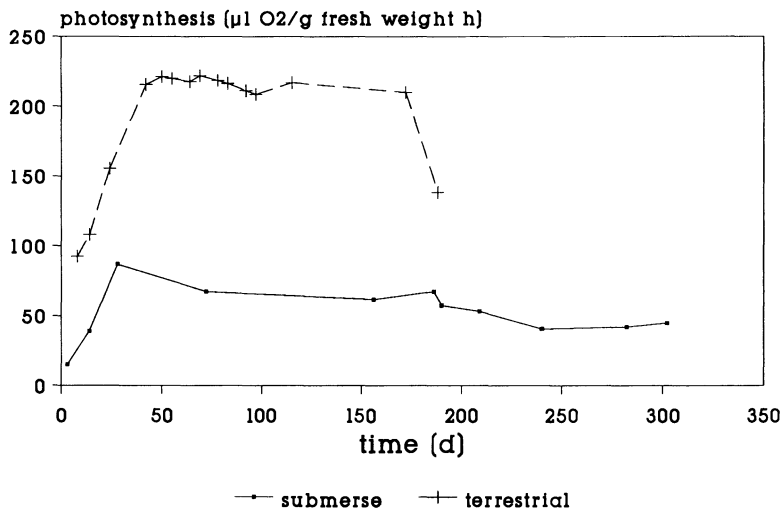—•— submerse   —+— terrestrial

FIGURE 4.   The photosynthetic O_2 production during the flood and the dry season in the várzea and igapó.

production due to net photosynthesis. The reduction of photosynthesis is faster and more intense in plants submerged in whitewater (Fig. 4 top). However, after 300 days of submergence, the leaf material still showed a slight net photosynthesis in the experiments. The dependence of the photosynthesis on regular rainfall during the terrestrial phase seems to be less pronounced than that of the root respiration. Hardly any effects of a water shortage on the rate of photosynthesis could be observed during the experiments.

The total chlorophyll content of the plants sub-merged in blackwater decreased relatively little during the period of flooding, remaining within the same range as during the terrestrial phase. In contrast, the leaves submerged beneath whitewater showed a reduction in their chlorophyll content, although the relative amount of chlorophyll in the leaves remained within the same range as that of the plants in the igapó (Fig. 5).

The concentration of soluble proteins in the cells reflects to some degree the metabolic activity. The quantitative determination of the fraction of soluble proteins revealed considerable differences in the con-

Várzea

chlorophyll a+b (mg/g fresh weight)

time (d)

Igapó

chlorophyll a+b (mg/g fresh weight)

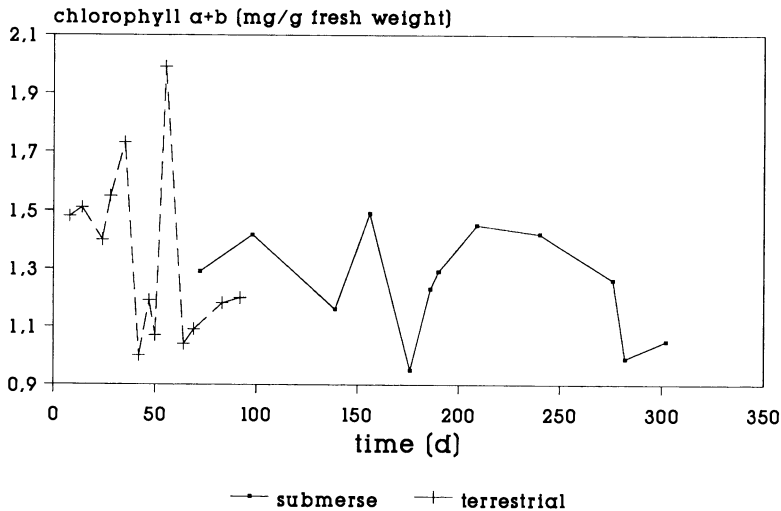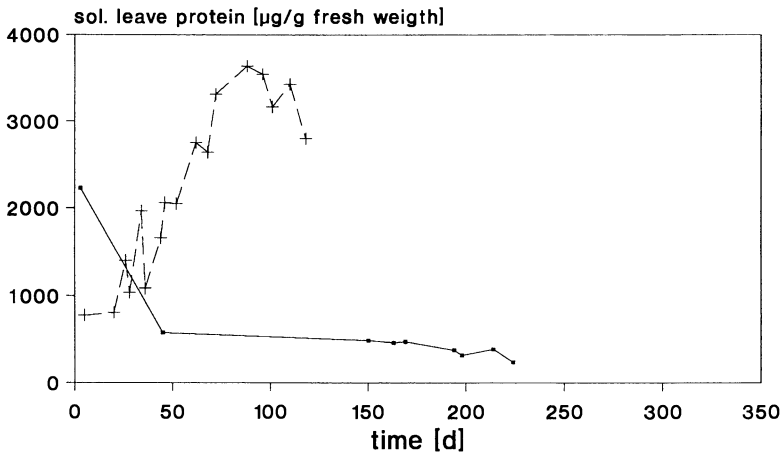time (d)
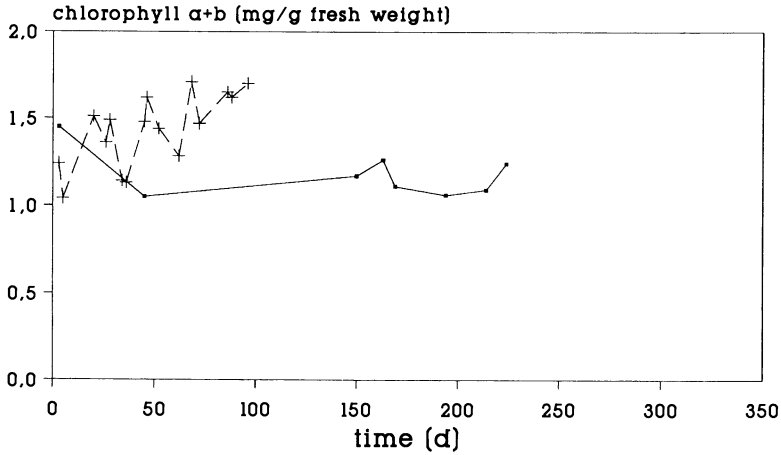
—•— submerse   —+— terrestrial

FIGURE 5.   The chlorophyll content of the leaves during the flood and the terrestrial phase in the várzea and igapó.

centrations within the plant material that was submerged compared to that which was not submerged. The difference was particularly pronounced in the leaves (Fig. 6). This difference was least noticeable in the roots of the plants from the igapó. The decrease in the protein content of the plant material examined is more or less continuous after a short period of inundation. However, a continuous submergence of more than 300 days does not reduce the content to an amount that would suggest that the cells are no longer capable of functioning. Similarly, a lack of rainfall during the terrestrial phase

might have a negative effect on the content of soluble proteins. The concentration of soluble proteins is greater, on the average, in the plants of the várzea than in those of the igapó. The relative amount of protein in the leaves is considerably greater than that in the roots (Fig. 6).

The metabolism of the *A. jauari* roots is modified during inundation, and ethanol begins to accumulate at the beginning of the aquatic phase (Fig. 7). As the inundation phase continues, however, the ethanol level in the roots is found to be only slightly elevated. This is especially true for the plants

Várzea

sol. leave protein [µg/g fresh weigth]

Igapó

sol. leave protein (µg/g fresh weight)
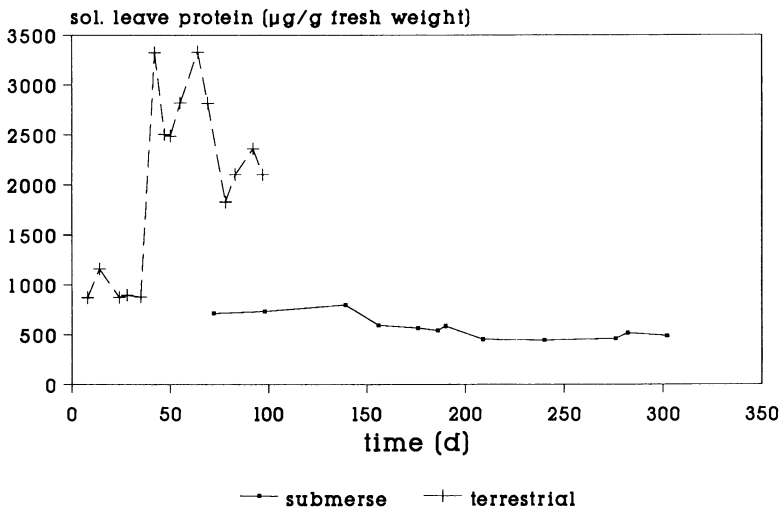

—•— submerse   —+— terrestrial

FIGURE 6.   Amount of soluble protein in the leaves during the flood and the terrestrial phase in the várzea and igapó.

growing in the igapó (Fig. 7). Relatively high concentrations encountered at the beginning of the emergent phase result from the waterlogged soil and the increased need for energy by the roots to support the growth that has already begun again. The increase in the ethanol content of the roots in the várzea (Fig. 7) at the end of the terrestrial phase can also be explained by the fact that the soil has become waterlogged.

Malate accumulates in the roots during the flood, and a relatively rapid increase in the concentration occurs during the first 40 days of inundation (Fig.

8). By the end of the flood period, even the roots of the plants in the várzea have developed a heavy accumulation of this metabolite (Fig. 8). During the terrestrial phase, the malate content of the roots in the igapó is subject to relatively strong fluctuations (Fig. 8). However, as in the case of the várzea plants, these concentrations are considerably lower than those recorded during the period of inundation. An accumulation of lactate and alanine due to inundation could not be detected, even after *A. jauari* had been submerged for more than 300 days.

During the period of inundation, the amount
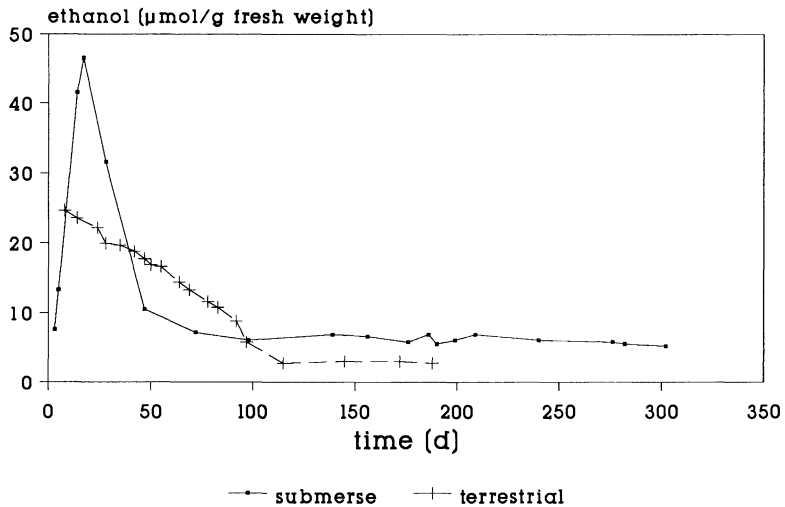
Várzea
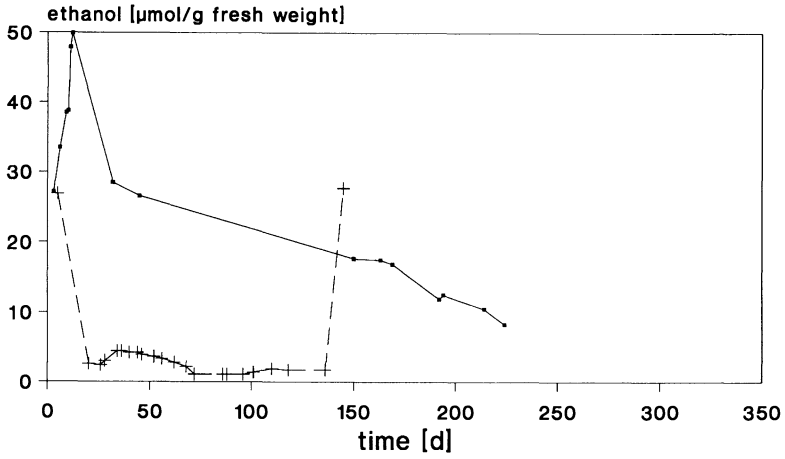
Igapó

FIGURE 7.   Accumulation of ethanol in the roots during the flood and the terrestrial phase in the várzea and igapó.

of nonstructural carbohydrates in the roots of *A. jauari* decreases by about 50 percent. The longer the plants are submerged, the lower is the carbohydrate content. The loss is more intensive among the plants growing in the várzea than those in the igapó. The amount of stored carbohydrates is relatively low, totaling about 300 mg per g of dry weight. During the terrestrial phase, the stored supply of carbohydrates is replenished to the amount reported above.

The water content of the plant tissue provides information on the amount of structural elements and the age of the organs, because the proportion

of dry material is lower in younger roots and leaves than in older ones. The average water content of the roots is higher than that in the leaves. During the inundation, the water content of the roots first decreases, then increases again at the time new root growth is observed. This is similar to the pattern observed during the terrestrial phase. In a way similar to the respiration decreases during periods of little rainfall as described above, the growth of the roots stagnates and their water content decreases. A lack of rainfall has scarcely any influence on the water content of the leaves. There is a slight increase in the amount of dry material in the leaves, which

Várzea

malate [μmol/g fresh weight]

Igapó

malate [μmol/g fresh weight]

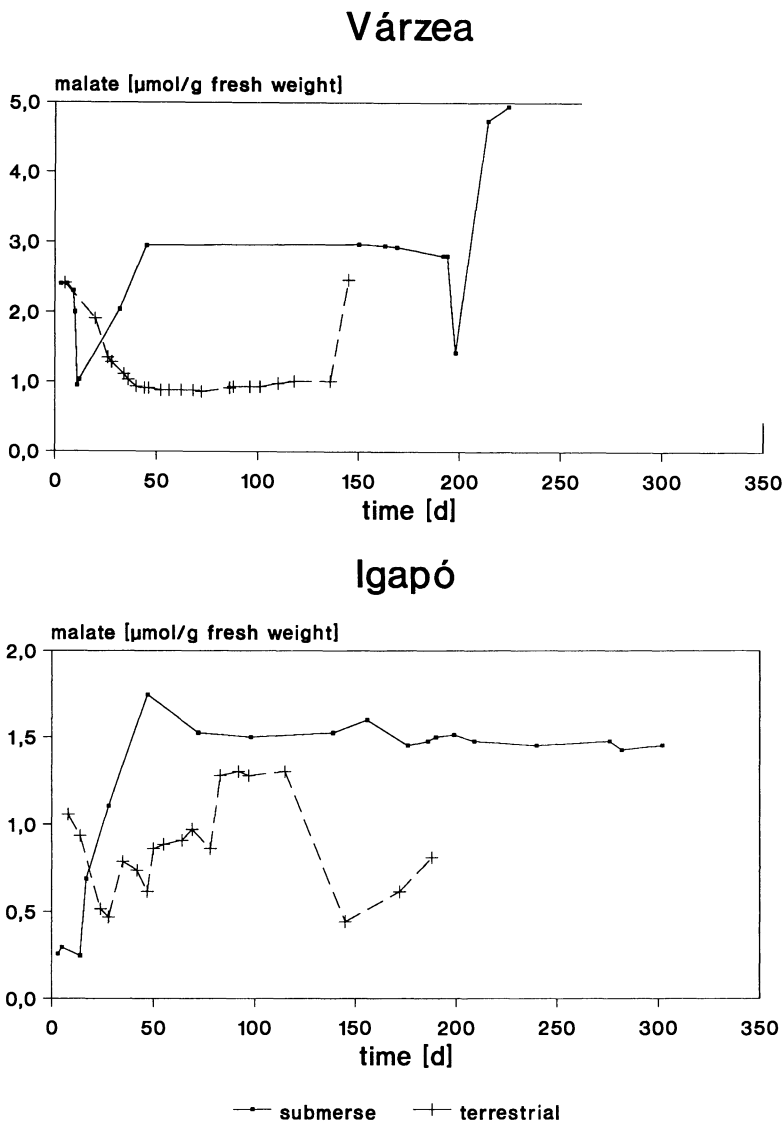

—•— submerse   —+— terrestrial

FIGURE 8.   Accumulation of malate in the roots during the flood and the terrestrial phase in the várzea and igapó.

is more or less related to age. During the inundation, this results from an increase in the degree of sclero-morphy, which is the formation of branching scler-eids in the mesophyll. These observations apply particularly to the plants in the igapó.

DISCUSSION

The increasing water content of the soil reduces the supply of available oxygen and thereby influences the root morphology of terrestrial plants. The result

is a reduction in the growth of the tap roots and an increase in the spreading and the number of branch roots in the upper layers of soil above the level where the partial pressure of oxygen is 0.01 to 0.03 atm at 20°C (Jackson & Drew 1984). *A. jauari* can survive with a shallow root system during shortage of oxygen caused by the flooding as well as by the lack of nutrients in tropical soils.

The hypoxia induced by flooding stimulates the formation of aerenchyme tissue (Armstrong 1971). The formation of this tissue seems to enhance the survival chances of many species in wetland habitats

(Kawase 1981). The very well-developed aeren-chyme tissue of A. jauari roots (Fig. 3) indicates an adaptation to the poor aeration of the soil. The lacunar aerenchyme in the roots of A. jauari is very similar to that tissue in Eichhornia crassipes and Phragmites australis. A well-functioning inner ven-tilation has been demonstrated for these plants, and there is even an exudation of oxygen into the sur-rounding medium (Jedicke et al. 1989, Gries et al. 1990), according to the findings of Carpenter et al. (1983) for the species Myriophyllum verticulatum. It is therefore likely that oxygen is also lost to the medium from the roots of A. jauari, thereby ex-plaining the availability of nutrients to the plant even during the submerged phase. Many nutrients are available to the roots only in the oxidized state.

The accumulation of ethanol in the roots of A. jauari during the period of rising water is considered to be a short-term adaptation to the lack of oxygen, because the transition to this kind of metabolism occurs very rapidly (Davies 1980). Joly and Craw-ford (1982) also described this phenomenon for newly germinated plants of various flood-tolerant tropical trees, and Monk et al. (1984) showed that it occurs in Schoenoplectus lacustris. According to Pearson and Havill (1988), a long-term conversion to this kind of metabolism has been described only for flood-tolerant species. If the period of submer-gence lasts longer than 30 days, the alcohol fer-mentation becomes unimportant for the breakdown of carbohydrates. The accumulation of organic acids and aerobic respiration, dependent on oxygen trans-port, begin to play the dominant roles at this stage.

The formation of lactate, to regenerate the re-duction equivalents during the submerged phase, as described by Joly and Crawford (1982), is in-significant in A. jauari. The same is true for alanine formation.

The accumulation of malate in the roots of A. jauari first shows a considerable increase, 10 days after the inundation, at the same time as the ethanol content starts to decrease. After 50 days of sub-mergence, the accumulation stagnates and does not begin again until after the flood waters have receded. Similar findings for Nyssa silvatica were reported by Keeley (1978), and Joly and Crawford (1982) also found that the elevation of the malate accu-mulation rate is only temporary in various tropical tree species. The reason for this malate accumulation cannot be due to the anaerobic pathway meeting the need for energy because this pathway, which as generally described is mediated by phosphoenol-pyruvate carboxylase, does not produce an energy gain. Pradet and Bomsel (1978) reported that the

advantage of this reaction is the fixation of CO_2 in in organic acid. This suggests that malate accu-mulation primarily serves to reduce the partial pres-sure of CO_2 in the aerenchyme of the roots. This gas is produced by the ethanol synthesis as well as by aerobic respiration. In A. jauari, it might also be a metabolic reaction that facilitates the absorption of O_2 in the lacuna system of the roots.

An important factor aiding the survival on an anaerobic biotope is the control and reduction of glycolysis, a process which permits a small gain of energy through a high consumption of reserve ma-terials. The respiration in the tissues of plants well-adapted to hypoxic conditions can proceed at an internal saturation of oxygen of only 0.05 percent. The maximum metabolic rates can be attained at saturations up to 20 percent (Armstrong & Gaynard 1976). A long-term response of Hymenaea courbaril is a reduction of the respiratory demand of the root system (Joly 1991). The oxygen consumption of A. jauari roots under water is reduced, but it does not completely cease. Similar observations have been made on other species e.g., Macrolobium acaciae-folium (Schlüter & Furch 1992). During submer-gence, there is an initial reduction in the respiration rate, but in experiments, the oxygen consumption increased again after a period of 10 to 20 days. Therefore, there must have been an improvement in the oxygen supply to the roots, even though there was no such improvement in the lower water layers. The simultaneous reduction in the ethanol content supports the assumption that the energy require-ments of the root tissue were not being met by glycolysis at that time.

The improvement in the oxygen supply could have resulted from a transport from the stems to the roots. The nature of the driving force for the movement of air from the leaves throughout the stems and into the roots and the processes control-ling this mechanism, whether diffusion or ventila-tion under pressure, remain unknown. Indirect in-dications of an oxygen transport were provided by the determinations of photosynthesis in the leaves under water. The photosynthetic activity increased again at about the same time during the experiments as the increase in the respiration rate was observed. Furthermore, the chlorophyll content of the leaves is hardly any lower than during the emergent phase after periods of submergence lasting over 300 days. It therefore seems very likely that photosynthetic reactions take place. The young A. jauari plants are adapted to extremely dim illumination. As plants of the understory, an illumination of only 30 to 280 μmols of photons per m^2 per sec is available

to the plants, depending on the location. Under water, a quantum density of minimal 3 μmols of photons per m^2 per sec is available to the plants that permits at least a low rate of photosynthesis. A quantum density under 10 μmols of photons per m^2 per sec is enough for a low photosynthetic activity (Oberbauer & Strain 1986). It has already been demonstrated that such photosynthesis is possible for another typical plant of the inundation forests, *Symmeria paniculata,* the leaves of which are capable of photosynthesis at depths up to 1.5 m below the surface (Fernandes-Corrêa & Furch 1992). The stabilization of the chlorophyll content in the chloroplasts under water also indicates that there is no significant degeneration of the pigment system.

Even for very low rates of photosynthesis, a functioning gas exchange is necessary. It has been demonstrated that the submerged leaves of *A. jauari* are not infiltrated by river water. This was shown by determinations using the pressure chamber method as well as through microscopic examination (Fernandes-Corrêa & Furch 1992, Schlüter 1989). An infiltration is prevented by the heavy deposits of epicuticular wax and the leaf spines, as well as by the chamber-like cavities formed by the cells surrounding the stomata. Thus, there is a layer of air on the lamina, as described by Jackson *et al.* (1987), through which a sufficient gas exchange for photosynthesis is possible, as shown by the model calculations of Schlüter (1989). The high partial pressure of CO_2, which is typical for the waters of the inundation forests, facilitates the transition of CO_2 into the gas phase. The resistance of the stomata is not great enough to prevent the continuous supply of CO_2 to the leaves (pers. obs.). Apparently, the mechanism of gas exchange under water is similar to but opposite from the plastron respiration known from animals.

A similar phenomenon was described by Gaynard and Armstrong (1987) for *Eriophorum angustifolium,* which, while fully submerged and under illumination of a constant intensity, is able to maintain a rate of photosynthesis dependent upon the physical concentration of CO_2 in the water. Thus, for the juvenile plants, the limiting factor for photosynthesis is not carbon dioxide but rather light. Further evidence for this is provided by the differences between the photosynthesis rates of the plants submerged beneath blackwater and whitewater. Because of the large amount of suspended matter in the whitewater, its transparency is considerably less than that of the blackwater (Furch *et al.* 1985). Furthermore, the plants in the igapó are found in more low-lying regions along the shore than those in the várzea. The reason for this could be the poorer transparency of the whitewater, which determines the limit for the settlement by the plants. This observation provides additional evidence that the quantum density under water determines the survival chances of the young plants.

In addition, it is shown that the energy reserves of the roots, stored in the form of carbohydrates, are still not exhausted after a period of over 300 days under water. Therefore, there is enough energy available to support the structure and the function in all parts of the plants, even those roots located in hypoxic layers.

The survival of the palm *A. jauari* during inundation seems to be possible by a flexible interaction of photosynthesis, respiration, and alcohol formation supported by a reversal of plastron respiration through the stomata and the fixation of CO_2 through malate formation in the roots. The free movement of gases throughout the whole plant stabilizes the interactions.

ACKNOWLEDGMENTS

LITERATURE CITED

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.
———, AND T. J. GAYNARD. 1976. The critical oxygen pressures for respiration in intact plants. Physiol. Plant 37: 200–206.
BERTANI, A., AND I. BRAMBILLA. 1982a. Effects of decreasing oxygen concentration on some aspects of protein and amino-acid metabolism in rice roots. Z. Pflanzenphysiol. 107: 193–200.
———, AND ———. 1982b. Effects of decreasing oxygen concentration on wheat roots. Growth and induction of anaerobic metabolism. Z. Pflanzenphysiol. 108: 283–288.

———, ———, AND F. MENEGAS. 1980. Effects of anaerobiosis on rice seedlings: growth, metabolic rates, and fate of fermentation products. J. Exp. Bot. 31(120): 325–331.

BRADFORD, M. M. 1976. A rapid and sensitive method for quantitation microgram quantities of protein utilizing the principle of protein Dye-Binding. Anal. Biochem. 72: 248–254.

CARPENTER, S. R., J. J. ELSER, AND K. M. OLSON. 1983. Effects of roots of *Myriophyllum verticillatum* on sediment redox conditions. Aqua. Bot. 17: 243–249.

CRAWFORD, R. M. M., 1966: The control of anaerobic respiration as a determining factor in the distribution of genus *Senecio*. J. Ecol. 54: 403–413.

———. 1971a. Some metabolic aspects of ecology. Trans. Bot. Soc. Edinb. 41: 309–322.

———. 1971b. Physiologische Ökologie: Ein Vergleich der Anpassung von Pflanzen und Tieren an sauerstoffarme Umgebung. Flora 161: 209–223.

DAVIES, D. D. 1980. The biochemistry of plants: metabolism and respiration, Vol. 2. Academic Press, New York. London, Sidney.

FERNANDES-CORRÊA, A. F., AND B. FURCH. 1992. Investigations on the tolerance of several trees to submergence in blackwater (igapó) and whitewater (várzea) inundation forests near Manaus, Central Amazonia. Amazoniana 11: 71–84.

FURCH, B. 1984. Untersuchungen zur Überschwemmungstolerance von Bäumen der Várzea und des Igapó. Biogeographica 19: 77–83.

———, A. F. FERNANDES-CORRÊA, J. A. S. N. DE MELLO, AND K.-R. OTTO. 1985. Lichtklimadaten in drei aquatischen Ökosystemen verschiedener physikalisch-chemischer Beschaffenheit. Amazoniana 9(3): 411–430.

———, AND C. STEINBERG. 1977. Extraktion freier Aminosäuren aus Pilzsporen (*Phycomyces blakesleanus*). Z. Pflanzenernähr. Bodenkd. 140: 531–541.

GABRIEL, A. 1983. Ammonium-Assimilation und Metabolismus der freien Aminosäuren bei *Sphagnum magellanicum* Bird. Ph.D. Thesis, University of Kiel, Kiel, Germany.

GAYNARD, T. J., AND W. ARMSTRONG. 1987. Some aspects of internal plant aeration in amphibious habitats. *In* R. M. M. Crawford. (Ed.). Plant life in aquatic and amphibious habitats, pp. 303–320. Blackwell Scientific Publications, Oxford, Boston, Melbourne.

GOULDING, M., M. LEAL CARVALHO, AND E. G. FERREIRA. 1988. Rio Negro, rich life in poor water. SPB Academic Publishing bv, Netherlands.

GRIES, C., L. KAPPEN, AND R. LÖSCH. 1990. Mechanism of flood tolerance in reed, *Phragmites australis* (Cav.) Trin. ex Steudel. New Phytol. 114: 589–593.

JACKSON, M. B., AND M. C. DREW. 1984. Effects of flooding on growth and metabolism of herbaceous plants. *In* T. T. Kozlowski (Ed.). Flooding and plant growth, pp. 47–128. Academic Press, New York, London, São Paulo.

———, J. WATERS, T. SETTER, AND H. GREENWAY. 1987. Injury to rice plants caused by complete submergence; a contribution by ethylene (ethene). Exp. Bot. 38(196): 1826–1838.

JEDICKE, A., B. FURCH, U. SAINT-PAUL, AND U.-B. SCHLÜTER. 1989. Increase in the oxygen concentration in Amazon waters resulting from the root exudation of two notorius water plants, *Eichhornia crassipes* (Pontederiaceae) and *Pistia stratiotes* (Araceae). Amazoniana 3: 411–430.

JOLY, C. A. 1991. Flooding tolerance in tropical trees. *In* M. B. Jackson, D. D. Davies, and H. Lambers (Eds.). Plant life under oxygen deprivation, pp. 23–34. The Hague, The Netherlands.

———, AND R. M. M. CRAWFORD. 1982. Variation in tolerance and metabolic responses to flooding in some tropical trees. J. Exp. Bot. 33(135): 799–809.

KAWASE, M. 1974. Role of ethylene in induction of flooding damage in sunflower. Physiol. Plant 31: 29–38.

———. 1981. Anatomical and morphological adaptation of plants to waterlogging. Hortic. Science 16: 30–34.

KEELEY, J. E. 1978. Malic acid accumulation in roots in response to flooding: evidence contrary to its role as an alternative to ethanol. J. Exp. Bot. 29(113): 1345–1349.

KLINGE, H. 1983. Forest structures in Amazonia. The Environmentalist 3(5): 13–23.

KOZLOWSKI, T. T. 1984. Extent, causes, and impacts of flooding. *In* T. T. Kozlowski (Ed.). Flooding and plant growth, pp. 1–9. Academic Press, New York, London, Toronto.

MONK, L. S., R. M. M. CRAWFORD, AND R. BRÄNDLE. 1984. Fermentation rates and ethanol accumulation in relation to flooding tolerance in rhizomes of Monocotyledonous species. J. Exp. Bot. 35(154): 738–745.

OBERBAUER, S. F., AND B. R. STRAIN. 1986. Effects of canopy position and irradiance on the leaf physiology and morphology of *Pentaclethra macroloba* (Mimosaceae). Am. J. Bot. 73(3): 409–416.

PAECH, K., AND M. V. TRACEY. 1955. Moderne Methoden der Pflanzenanalyse, Vol. 2. Springer Verlag, Berlin, Göttingen, Heidelberg.

PEARSON, J., AND D. C. HAVILL. 1988. The effect of hypoxia and sulphide on culture-grown wetland and non-wetland plant. II. Metabolic and physiological changes. J. Exp. Bot. 39(201): 431–439.

PONNAMPERUMA, F. N. 1977. Physicochemical properties of submerged soils in relation to fertility. IRRI Res. Paper Ser. 5.

PRADET, A., AND J. L. BOMSEL. 1978. Energy metabolism in plants under hypoxia and anoxia. *In* D. D. Hook and R. M. M. Crawford (Eds.). Plant life in anaerobic environments, pp. 88–118. Ann Arbor. Science, Michigan.

PRANCE, G. T. 1979. Notes in the vegetation of Amazonia, III. The terminology of Amazonian forest types subject to inundation. Brittonia 31: 26–38.

SCHLÜTER, U.-B. 1989. Morphologische, anatomische und physiologische Untersuchungen zur Überflutungstoleranz zweier charakteristischer Baumarten (*Astrocaryum jauari* und *Macrolobium acaciaefolium*) des Weiß-und

Schwarzwasserüberschwemmungswaldes bei Manaus.—Ein Beitrag zur Ökosystemanalyse von Várzea und Igapó Zentralamazoniens. Ph.D. Thesis, University of Kiel, Kiel, Germany.

————, AND B. FURCH. 1992. Morphologische, anatomische und physiologische Untersuchungen zur Überflutungstoleranz des Baumes *Macrolobium acaciaefolium,* charakteristisch für die Weiß- und Schwarzwasser—Überschwemmungswälder bei Manaus, Amazonas. Amazoniana 12(1): 51–69.

SENA GOMES, A. R., AND T. T. KOZLOWSKI. 1988. Physiological and growth responses to flooding of seedlings of *Hevea brasiliensis.* Biotropica 20(4): 286–293.

ZIEGLER, R., AND K. EGLE. 1967. Zur quantitativen Analyse der Chloroplastenpigmente. I. Kritische Überprüfung der spectralphotometrischen Chlorophyllbestimmung. Beitr. Biol. Pflanz. 4: 39–63.