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Investigations on the tolerance of several trees to submergence in blackwater (Igapó) and whitewater (Várzea) inundation forests near Manaus, Central Amazonia

by

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Abstract

Physiological, cytological, and anatomical studies were carried out on the tolerance of trees to submergence in blackwater and whitewater inundation forests, locally called Igapó and Várzea, respectively. For this purpose, the leaves of several abundant tree species were investigated to determine their functional capability after submersion during the inundation phase. Their performance was compared with that of genetically identical leaves on the same branch that had sprouted after the flood waters had receded.

The studies showed that, in spite of submersion for up to several months and sometimes even in spite of the fact that they were still partially under water, these leaves had full functional capability at the beginning of the terrestrial phase, as determined by examination under the light and scanning electron microscope, the water potential, and the CO_2 exchange.

Keywords: **Amazonia, floodplains, trees, leaves, water potential, photosynthesis.**

This study is dedicated to Professor Dr. Harald Sioli in commemoration of his 80th birthday.

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Introduction

A series of biological peculiarities can be expected in the transition zone between land and water whenever there is a regular periodic fluctuation between terrestrial and aquatic phases. To better describe this phenomenon, the flood-pulse concept was formulated by JUNK et al. (1989).

Because of the great differences in the amounts of water flowing through the river system during the course of the year, the Amazon region has the most extensive inundation area in the world. It encompasses those along blackwater rivers, such as the Rio Negro, and whitewaters, including the Rio Solimões or Amazon.

In central Amazonia, the complex structures of the ecosystems are characterized by biota influenced by changes in the water level that can be depicted as a sine curve completing a full cycle in one year and having an amplitude of over 10 m, as recorded at Manaus.

Figure 1 depicts the conditions to which the vegetation is exposed during a normal annual cycle. The upper parts of the larger trees in the inundated forests remain above the flood waters, while young trees of the same species and the shrubs remain fully submerged up to several months each year.

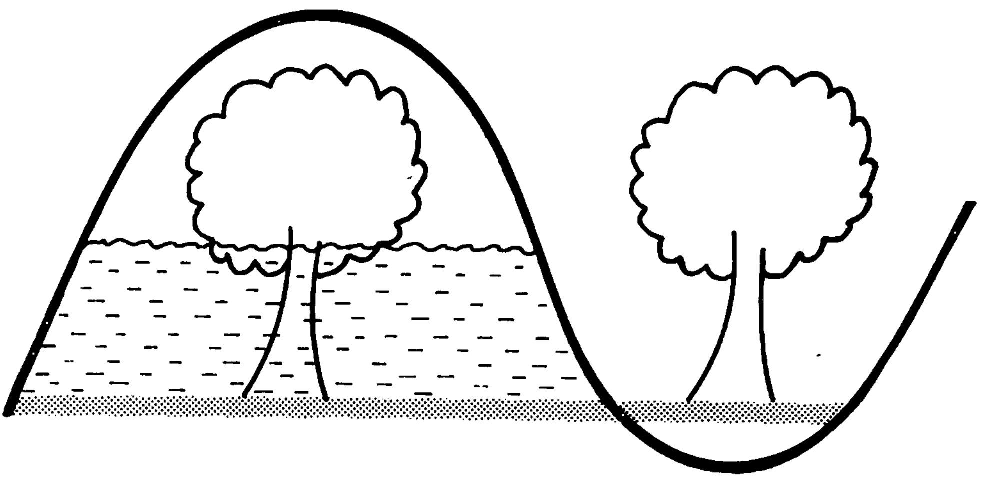


Fig. 1:
Picture showing the whitewater inundation forest, or Várzea, and the blackwater forest, or Igapó. Normally, the riverside plains are flooded for about half of the year, and the understory is totally submerged. However, at some locations, flooding lasts for more than one year (according to K. FURCH).

Surprisingly, some of the plants display no scotomorphogenesis induced by the lack of light during the flood periods. At least some of their leaves are not shed, and these retain their structure and functional capability throughout much of the returning terrestrial phase (FURCH 1984; SCHLÜTER 1989; SCHLÜTER & FURCH in press). While submerged, the leaves are exposed to a hypoxid or even anoxic environment. This raises the question of how the metabolism of the trees continues under anaerobic conditions. Recently, tropical trees adapted to flooding have been subject to an increasing number of investigations (JOLY & CRAWFORD 1982). However, these investigations have dealt with relatively short-term inundation in comparison with that in Central Amazonia, and since only the roots of these trees were under water, the results are not applicable to plants growing under the conditions in the central Amazon region.

Material and methods

The species studied were growing in the blackwater inundation forest, called Igapó, of Tarumã Mirím and a flooded whitewater forest, called Várzea, on the Ilha de Marchantaria. Both forests are located near Manaus (Fig. 2).

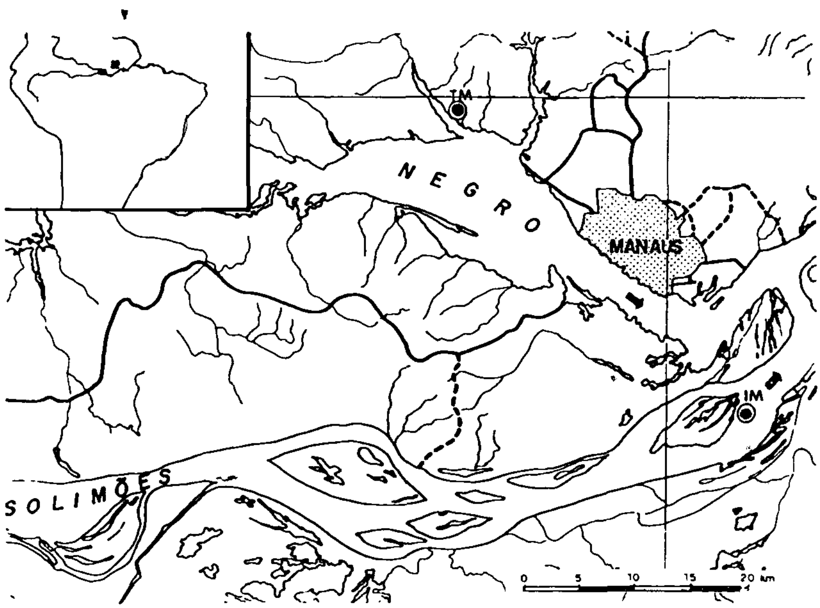


Fig. 2:
Map of the white- and blackwater flood plains in the catchment areas of the Rio Solimões (Amazon) and Rio Negro at their confluence near Manaus, Brazil, at 60°W, 2°S.

The characteristics of the forests were described by KLINGE (1973), PRANCE (1979), and WORBES (1983).

The plants investigated were 1 to 3 m high and belonged to the following species:

1. In the Igapó - *Eugenia inundata* (Myrtaceae), Lecythidaceae sp. indet., *Bactris* sp. (Arecaceae), Lauraceae sp. indet., *Acmanthera latifolia* (Malpighiaceae), *Symmeria paniculata* (Polygonaceae), and *Mabea nitida* (Euphorbiaceae).

2. In the Várzea - Rubiaceae sp. indet., *Tabernamontana* sp. (Apocynaceae), *Annona* sp. (Annonaceae), *Neolabatia cuprea* (Sapotaceae), *Crescentia amazonica* (Bignoniaceae), and *Gustavia augusta* (Lecythidiaceae).

The plants were growing at the location where a long-term inundation of several meters would cover them each year. Examinations with the light microscope were made using fresh material in the field. The scanning electron microscope (LEITZ 1000) was used to examine material fixed in 70 % alcohol at a later time.

The water potential was determined using a Roth pressure chamber according to the method of KREEB (1977). The error in this apparatus should amount to 1 bar (0.1 MPa). Three determinations were made on each object to arrive at a mean value. All determinations were made between 10 a. m. and noon, because during this time, the greatest difference between the species could be expected.

In the case of two species, *Symmeria paniculata* and *Bonafousia muricata*, the results were checked using a gas analyzer (IRGA LCA-2, ADC air supply, and PARKINSON Leaf Chamber) in order to ascertain whether the leaves still showed photosynthetic activity after spending several months beneath the flood waters and then being exposed again to the atmosphere.

Results

After inundation for as long as several months, the leaves still on the trees appear intact. Some of those in the Várzea are only lightly coated with sediment, while some in the Igapó are covered only by spicules from freshwater sponges. They usually appear darker than the genetically identical leaves that subsequently sprout. Two reactions are known to contribute to this differences in appearence: the total chlorophyll content of some leaves increases under water (FURCH 1984), while the intercellular spaces of others are reduced (SCHLÜTER 1989). In no cases were the leaves infiltrated with water, as postulated by SCHOLANDER & DE OLIVIERA PEREZ (1968). An examination of the leaves under the light microscope provided no indication of this. Furthermore, the observation that leaves previously underwater could survive and remain functional during the subsequent terrestrial phase indicted that a filling of the intercellular spaces with water was unlikely. If they had been infiltrated with the flood waters, the gas exchange and mineral supply would have been prevented. If the assumptions of SCHOLANDER & DE OLIVIERA PEREZ (1968) had been correct, a resorption of the water that had infiltrated the leaves would have been necessary after the plants were again exposed to the air by the receding floods, and such a process on the scale necessary under the circumstances is difficult to conceive of.

The leaf surfaces of more than 20 species of tree that commonly occur in the Igapó and Várzea near Manaus were analyzed under a scanning electron microscope, and it was shown that the epidermal surface is structured similar to that of rice plants (JACKSON et al. 1987). This structure permits a film of air do adhere to the surface when the leaves are first submerged at the beginning of the aquatic phase. The following morphological arrangements make the displacement of the air remaining in the leaf and an infiltration of the ambient water extremely unlikely: recessed stomata surrounded by large, epicuticular wax concretions, as observed in *Mabea nitida* (Fig. 3); stomata surrounded by a wreath of giant cells and thereby kept recessed beneath the level of the remaining leaf surface, as in *Franchetella crassifolia* (Fig. 4); stomata with a dome--shape central stoma formed of a cuticular welt that produces a large antechamber, as in *Eugenia inundata* (Fig. 5); stomata bordered by thick wax layers, such as in *Symmeria paniculata* (Fig. 6).

It is a more probable assumption that the air around the stomata is retained in the form of bubbles and that gas exchange between the water and the trapped air takes place during submergence. This would be promoted by the partial pressure of CO_2 that often prevails in the water bodies (K. FURCH pers. comm.). At such pressure, CO_2 can leave solution and enter the leaf openings in the form of gas. Thus, a small amount of photosynsthesis would be possible under water. A quantum density of only a few $\mu mol/m^2 \cdot s$ would be sufficient for this to occur (FURCH et al. 1985).

Figs. 3-6: Scanning electron micrographs of the hypostomatic epidermal layers showing the stomata and epicuticular wax layers.

Fig. 3:
Mabea nitida: Wax concretions.

In March and August of 1967, SCHOLANDER & DE OLIVIERA PEREZ (1968) punctually determined the water potential of several species characteristic of the Igapó downstream from the confluence of the Rio Branco and Rio Negro. We made similar determinations during the months from May through November 1985 in the Igapó of Tarumã Mirím at about 11 a. m., during periods of bright sunshine and of overcast (Fig. 7). Some of the species from which leaves were sampled were the same as those investigated by SCHOLANDER & DE OLIVIERA PEREZ (1968). The leaves included some that had been submerged during the period of flooding and others that had sprouted since the flood waters had receded. Leaf samples were taken from the same tree 20 cm below and 20 cm above the water surface. The leaves that were still submerged had been under water for various periods of time, depending on the terrain elevation; the maximum period was more than six months. Of course, those leaves that had already emerged from the flood waters had been submerged for somewhat shorter periods of time. All samples were taken while the roots of the trees were still under water.

1. Leaves attached 20 cm above the surface of the water:

As in the investigations by SCHOLANDER & DE OLIVIERA PEREZ (1968), the values we recorded were between -5 and -22 bar, equivalent to -0.5 and -2.2 MPa. Neither significant differences in the potential or tendencies toward such differences were observed between leaves that had been submerged (O) and those that had newly sprouted (N). The weather conditions also had no observable effect. Generally, all potentials recorded were surprisingly low for plants rooted below the water level at the time of the determinations.

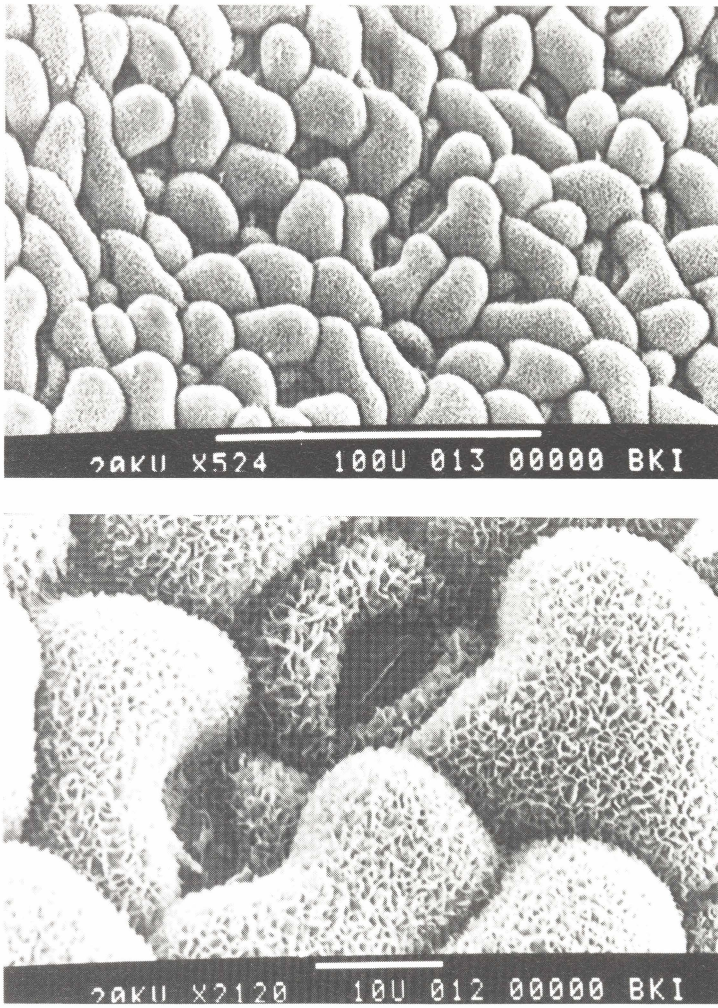


Fig. 4:
Franchetella crassifolia: stomata surrounded by giant cells.

2. Leaves taken 20 cm below the surface of the water:

The tendency toward a low water potential in spite of the best supply of water to the roots was also observed among these leaves. In no case was a potential of O or any positive value ever recorded, even when xylem water flowed from the place at which the leaf was separated from the stem, as reported by SCHOLANDER & DE OLIVIERA PEREZ (1968). The values are clearly in the negative range between -2 and -8 bar, equivalent to -0.2 and -0.8 MPa.

Fig. 5:
Eugenia inundata: stomata with large antechambers.

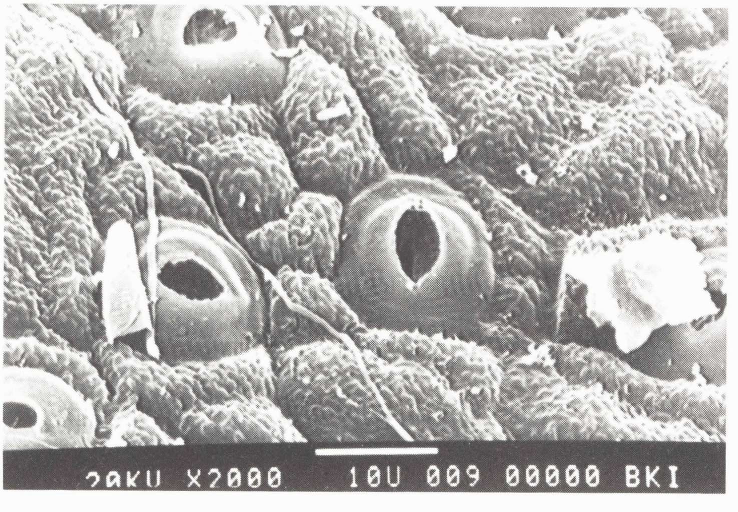


Fig.6:
Symmeria paniculata: stomata bordered by wax layers.

After the flood waters have completely receded from the terrain, those leaves that had been submerged for several months had a significantly lower water potential than otherwise identical leaves that were only a few weeks old. In Figure 8, the water

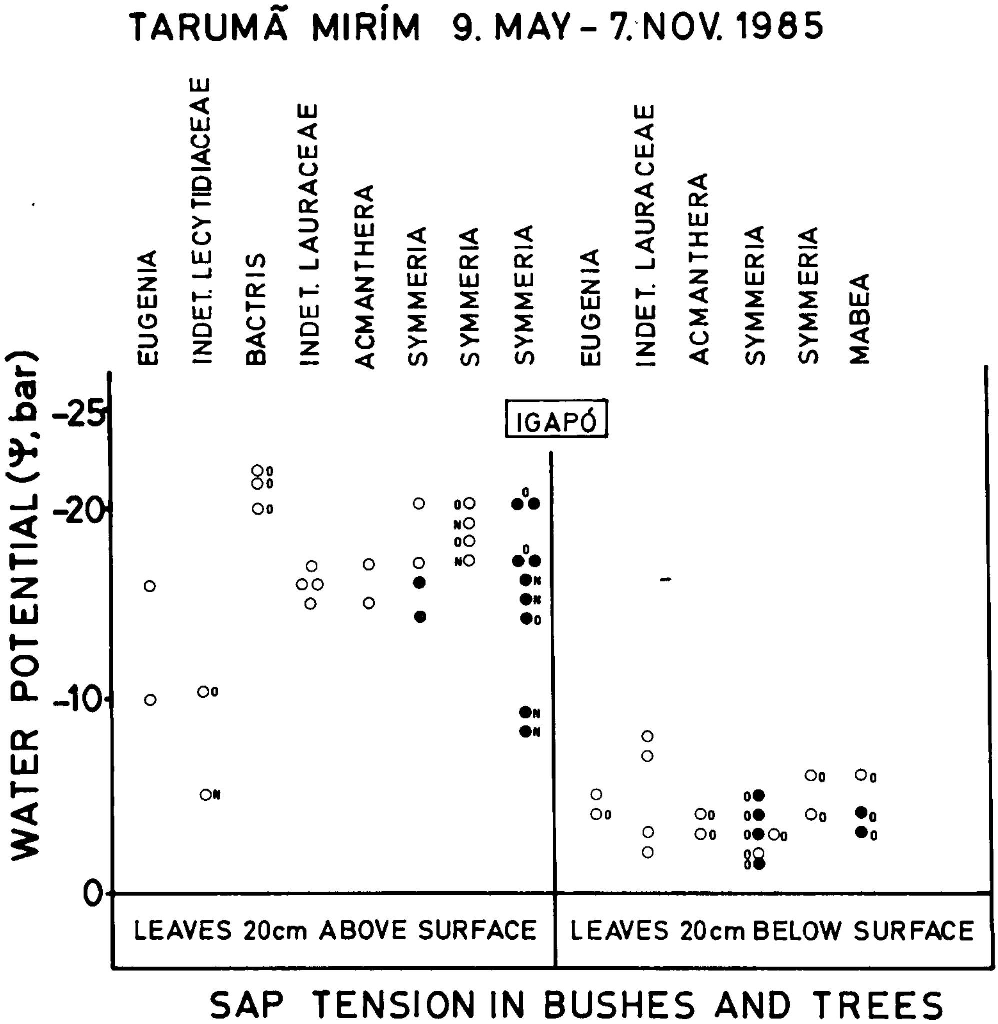
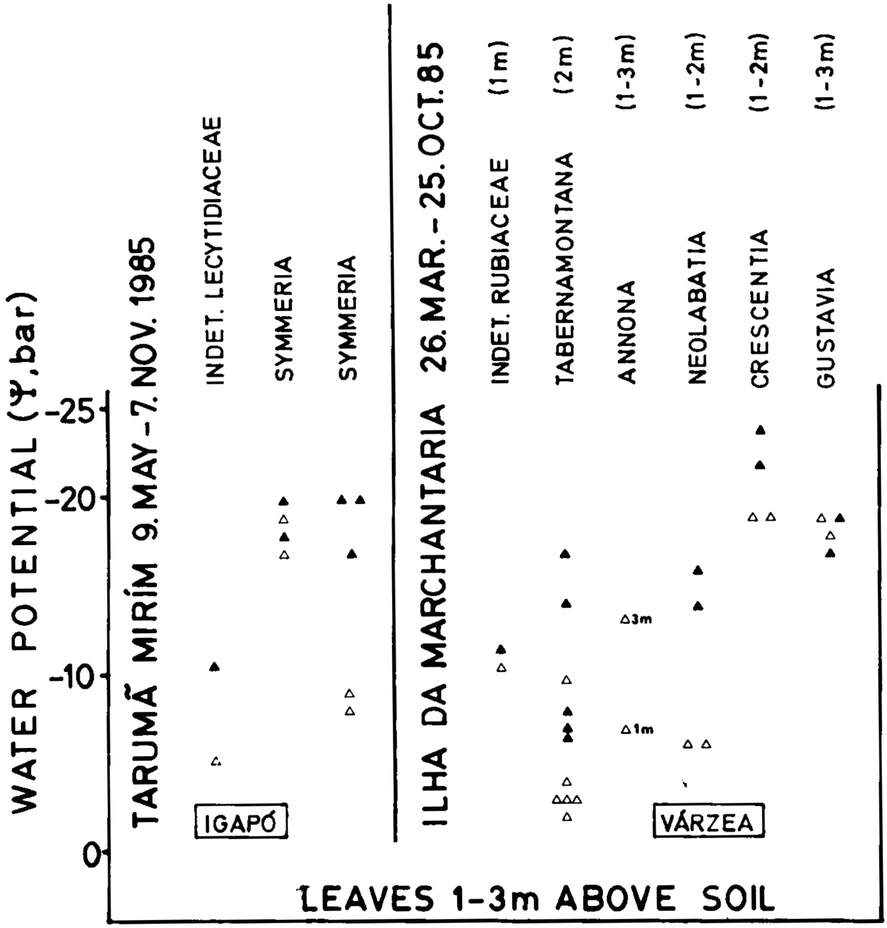


Fig. 7:
Water potential of several species in the Igapó forest near Manaus. O = old leaves that survived the inundation phase; N = mature leaves, recently sprouted; o = sunshine; ● = overcast.

potential values of several broadleaf, woody plants that frequently occur in blackwater and whitewater inundation forests are depicted. They are all in the range between -2 and -24 bar (-0.2 to -2.4 MPa), which is typical for mesophytes. The values for the individual species vary, apparently with the weather conditions or due to individual differences. However, it was evident that the 12 month old leaves, which had been submerged several meters deep for several months, always had lower water potentials than genetically identical leaves of the same species that were only a few weeks old. That was observed both in the Igapó of Tarumã Mirím and in the Várzea on the Ilha de Marchantaria. This difference may be influenced by the age of the leaves, which, however,



SAP TENSION IN BUSHES AND TREES

Fig. 8:
Water potential of several species in the Igapó and Várzea forests near Manaus. ▲ = old leaves that survived the inundation phase; Δ = mature leaves, recently sprouted; m = meters above the soil.

seems to have no significant effect on their functional capability, since their photosynthetic production must supply the biomass for the newly sprouting leaves.

Discussion

Generally, the water potential of the leaves is influenced by atmospheric, osmotic, and matrix potentials as well as the turgor of the mesophyll, the flow resistance within the entire plant, and the water potential of the soil. Single determinations are not sufficient to permit descriptions of the hydrological budgets of the entire plants. The main advantage of the pressure chamber method is its capability of providing values for important parameters immediately in the field (RITCHIE & HINCKLEY 1975). In combination with other observations, this parameter provides a basis for judging the functional capability of the leaves. In this way, it can be determined whether a leaf exposed to extreme environmental conditions, such as submersion for several months, has survived as a photosynthetic organ or has been lethally damaged.

In this investigation, functional capability of leaves that had been submerged for several months was determined during the transition from the aquatic to the terrestrial phase. This was true even though the previously submerged leaves had a considerably lower water potential than those that had newly sprouted during the terrestrial phase. This lower potential might be due to the generally observed decrease in stomatic activity that occurs as leaves become older (WARDLE & SHORT 1983). It should be noted that the age of as much as 13 months reached by leaves in central Amazonia is considerably greater than that attained by leaves in the temperate zones (MEDINA 1984). A second reason for the lowered water potential could be negative effects of the sediment coat in the Várzea or the sponge spicules in the Igapó. These coatings are quite frequently observed and easily visible. Damage due to fungus infiltration can be ruled out. Although hyphae are sometimes observed on the epidermis of the leaves during the aquatic phase, their intrusion into the stomata in this layer was seen only very rarely.

Damage of the mesophyll due to microbial decomposition processes was never observed. The leaves that survived the aquatic phase were just as functionally capable as those that sprouted later. This was further demonstrated by their chlorophyll content, which was normal (FURCH 1984). It can therefore be concluded from all observations and determinations yet described, that at least the majority of the leaves not shed at the beginning of the inundation remain functionally capable, at least when the water depth at which they remain does not exceed 1.5 m (FURCH 1984; SCHLÜTER & FURCH in press). It must still be determined whether the air trapped by the wreaths of cells surrounding the stomata, the antechamber formed by their raised borders, or the epicuticular wax faciliates a gas exchange between the ambient water and the leaf. Observations that some of the stomata are not closed under water and the relatively slight stomatic resistance of these leaves make it seem probable that there is a gas exchange at the interface between the water and air. This was calculated by SCHLÜTER (1989) and SCHLÜTER & FURCH (in press) for two species of plant that occur both in the Igapó and the Várzea, *Astrocaryum jauari* (Arecaceae) and *Macrolobium acaciaefolium* (Leguminosae). The exchange is promoted by the high partial pressure of CO_2 that is usually encountered under water in the inundation forests. This is sufficient to permit CO_2 from the water to pass through the stomata in the gas phase. SCHLÜTER (1989) calculated that there would be an influx of CO_2 amounting to several hundred $\mu l/cm^2 \cdot hour$. A similar phenomenon known from the animal kingdom is plastron breathing. We postulate that there is a gas exchange mechanism through the stomata under water in the opposite direction, and we propose two provisional names, "reverse plastron respiration" and "plastron photosynthesis", for this process. According to calculations based on leaf structure and the density of the stomata, which are not described in further detail here, an influx of about 200 μl $CO_2/m^2 \cdot hour$ would be possible for two species that are very abundant in the Igapó: *Symmeria paniculata*

(Polygonaceae) and *Bonafousia muricata* (Apocynaceae). This influx would make photosynthesis under water possible, though the amount would be rather small.

A prerequisite for this would be a sufficient quantum density (PAR). According to FURCH et al. (1985), this prerequisite would be met to a depths of several meters in the Igapó and to 3 m in the Várzea, if the tripton of the whitewater would sediment out. The elimination of this material by settling often occurs, and this probably be considered the usual case.

The photosynthesis determinations of *Symmeria paniculata* and *Bonafousia muricata* were performed using an infrared gas analyzer. The leaves analyzed were those on a *Symmeria paniculata* tree in the Igapó of Tarumã Mirím with a crown 11 m high. During autumn 1985, 4 m of the crown was under water, and 7 m was already above the water level. Branches were taken from this tree at water depths of 1 and 3 m below the water level and 1 m above. The amount of photosynthesis by both the submerged leaves and those exposed to the air was recorded immediately with the infrared gas analyzer. For technical reasons, all three samples were determined in an air-filled leaf chamber. If the photosynthesis of the leaves above the water level at the ambient quantum density of 1700 $\mu mol/m^2 \cdot s$ (PAR, cosine corrected sensor) is considered 100 %, then that of the leaves 1 m below the surface of the water also exposed to 1700 $\mu mol/m^2 \cdot s$ in the air would be over 20 %. Although the amount of photosynthesis could not be determined directly under water, it can be expected that a similar amount but possible less occurs under water. This indirect indication of photosynthesis under water is supported by the finding that the leaves taken at a depth of 3 m showed no indication of photosynthesis at all. It is therefore apparent that the quantum density recorded with an underwater sensor at the location these *Symmeria paniculata* leaves were taken, 10 $\mu mol/m^2 \cdot s$ at a depth of 3 m, was too low to permit a net photosynthesis to occur. From all of the results already obtained, we can assume that even under these conditions, there is a gross photosynthesis, but it is masked by the respiration of the leaves. Therefore, a value cannot be obtained with the infrared gas analyzer.

In Addition, branches were taken from a *Bonafousia muricata* tree in the Igapó during late summer of 1985. These branches were beneath 20 cm of water, and their branches had been submerged for about five months at the time. The branches were placed in plastic bags filled with blackwater and sent to Kiel, Germany. After removal from the water, determinations were made using a stationary gas analyzer. Although some of the conditions were not physiologically conducive, the leaves still showed a slight photosynthetic activity about 100 hours after the sampling in the field. This is also an indication that even under water, photosynthesis occurs, and considering all observations already made, at least these submerged leaves were capable of photosynthesis. That means that their structure and cytology permit such complex functions after such a long period under water.

Summary

Investigations on the tolerance of woody plants to submergence were conducted using leaves from two kinds of inundation forest, one in a blackwater region, the Igapó of Tarumã Mirím, and the other in a whitewater forest, the Várzea on the Ilha de Marchantaria, both located in Central Amazonia near Manaus.

The water potential of the leaves that had been submerged for several months during the aquatic phase was similar to that of the leaves that had recently sprouted during the terrestrial phase. The potential was in

the range normal for mesophytes, -2 to -24 bar. As expected, differences were found only for the age of the leaves and the height of their insertion.

Contrary to previous assumptions but in accord with theoretical calculations, the potential of leaves that were still under water at the time of sampling was always less than 0 and therefore never positive. The most extreme negative value recorded for these was -8 bar.

Consequently, no indications were found during light or scanning electron microscopic examination that water was infiltrating the leaves. The stomata are protected by heavy epicuticular waxes or by a wreath of cells against infiltration by water. Furthermore, in the antechamber region of the stomata, the trapped air permits a low level of photosynthesis to occur under water in the presence of a sufficient light quantum density. The rate of photosynthesis could be determined by model calculations and by actual determinations of the gas exchange by two species of plant.

From the observations, it can be generally concluded that the structure and functional capability of tree leaves that are not shed during submersion can be retained beneath at least 1 m of blackwater, and a slight rate of photosynthesis can be maintained faciliated by a kind of "reverse plastron respiration". The metabolic processes are expressed by the clearly negative water potential of the submerged leaves ranging from -2 to -8 bar.

Zusammenfassung

Untersuchungen zur Überschwemmungstoleranz von Laubgehölzen wurden an deren Blättern in zwei Überschwemmungswäldern, einem Schwarzwasserüberschwemmungswald (Igapó des Tarumã Mirím) und einem Weißwasserüberschwemmungswald (Várzea auf der Ilha de Marchantaria) in Zentralamazonien bei Manaus gemacht.

Die Untersuchungen umfaßten Messungen von Wasserpotentialen, - lichtmikroskopischer und elektronenmikroskopischer (REM) Art - und bei zwei Arten die Bestimmung der Photosyntheseleistung.

Die Wasserpotentiale von Blättern, die monatelang unter Wasser während der aquatischen Phase waren, lagen im Bereich derer von in der terrestrischen Phase geschobenen Folgeblättern; man erhielt dadurch Potentiale, die die Pflanzen als Mesophyten auswiesen (-2 bis -24 bar; -0,2 bis -2,4 MPa). Es ergaben sich erwartungsgemäß Unterschiede hinsichtlich des Alters und der Insertionshöhe der Blätter.

Entgegen bisheriger Annahme, jedoch in Übereinstimmung mit theoretischen Kalkulationen waren die Potentiale der Blätter, die sich bei der Entnahme noch unter Wasser befanden, immer kleiner als Null, also nie positiv. Im Extrem wurden hier Werte bis -8 bar (-0,8 MPa) gemessen.

Folgerichtig ergab sich auch kein Hinweis (Lichtmikroskopie und Rasterelektronenmikroskopie) auf eine Infiltration der Blätter. Die Spaltöffnungen sind durch starke epicuticuläre Wachse, tiefe Vorhöfe und/oder hohe Kranzzellen nicht nur vor einer Infiltration unter Wasser geschützt, sondern die im Vorhofbereich der Stomata festgehaltene Luft ermöglicht auch unter Wasser bei entsprechender Quantenstromdichte eine geringe Photosyntheserate, wie durch Messungen des Gasaustausches und durch Modellrechnungen für zwei Arten wahrscheinlich gemacht werden konnte. Die Photosynthese unter Wasser wird somit durch einen Gasaustauschmechanismus ermöglicht, den man als "reverse Plastronatmung" bezeichnen könnte. Nach den Beobachtungen ist generell davon auszugehen, daß Blätter von Bäumen, die diese unter Wasser nicht abwerfen, zumindest bis zu einer Überschichtung mit Schwarzwasser bis zu 1,5 Meter Struktur und Funktion durch eine geringe Photosyntheserate erhalten können; Ausdruck dieser Stoffwechselprozesse ist ein deutlich negatives Wasserpotential auch bei submersen Blättern.

Resumo

Experiências para analisar a tolerânciade de árvores em relação à inundação foram feitas em folhas de duas florestas que sempre inundam, uma nas águas pretas do igapó do Tarumã Mirím e outra nas águas

brancas da várzea da Ilha de Marchantaria, ambas perto de Manaus, na Amazônia Central. As experiências incluem mediçoes de potências de água, análises de microscópio normal e electrônico e com duas espécies a determinação da realização da fotosíntese.

O potêncial de água de folhas que ficaram durante meses na época de cheia ambaixo da água esta à mesma altura do potencial de folhas de sucessao da época de baixa; os potênciais medidos caracterizam as plantas como mesófitas (-2 até -24 bar, -0,2 até -2,4 MPa). Como é de se esperar existem diferenças quanto à idade e à altura da inserção das folhas. O potêncial das folhas que se encontravam embaixo da água na hora da colheita é sempre, ao contrário do suposto, mas de acordo com cálculos teóreticos, menos que zero, nunca positivo. Em casos extremos foram medidos valores até -8 bar (- 0,8 MPa).

Consequentemente nao houve nenhuma indicação microscópica de infiltração nas folhas. Os estômatas não são só protegidos da infiltração por causa da vasta cêra epicuticular, dos vestíbulos profundos e/ou das altas células em coroa, mas o ar detido no vestíbulos dos estômatas possibilita também embaixo da água uma pequena quota de fotosíntese quando a densidade da corrente das quantas é adequada, como mostram mediçoes da troca de gases com cálculos-modelo em duas espécies.

Em sumo, a fotosíntese embaixo da água é possibilitada por um mecanismo de troca de gases que poderíamos chamar de "respiração de plastrao reversa".

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