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Adaptability of the fine root system of *Ceiba pentandra* (L.) Gaertn. to various sites of central Amazônia, Brazil*

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Summary

Ceiba pentandra (L.) Gaertn. (sumaúma), an economically important tree species in central Amazônia, stands out on account of its considerable ecological capacity of adapting to different site conditions. It can survive under seasonally dry conditions on terra firme as well as in the seasonally inundated várzea. Particularly the fine roots can structurally adapt to different soil conditions. The adaptation of the fine roots to terra firme condition results in the formation of an aerenchyma consisting of only small intercellular canals. During the dry months the walls of the epidermis cells increase in thickness and moreover they lignify and the exodermis suberize to prevent drainage. On the other hand the fine roots growing on várzea sites form lysigenously an aerenchyma consisting of extended and large intercellulars both within the cortex and the central cylinder. This large intercellular system supplies the plant with water and mineral elements and maintains the oxygen supply enabling photosynthesis throughout the year. In addition, above the soil surface numerous adventitious roots grow during the inundation period developing only small intercellular spaces within the cortex. Suberization is missing and only the primary xylem lignifies.

A simulation of the fine root study under similar growth conditions in a tropical greenhouse completely confirmed the structural adaptations of the fine roots to dry and seasonally inundated conditions. This ecological amplitude is important for the selection of *Ceiba pentandra* for sustainably managed forestry systems.

Introduction

Studies of the structural adaptability of the fine roots under conditions characterized by restricted oxygen supply during seasonally inundation were carried out mostly with herbaceous plants such as with *Eriophorum angustifolium* Honck. (Armstrong and Gaynard, 1976), *Oryza sativa* L. (Armstrong and Webb, 1985) and several other species (e.g. Smirnoff and Crawford, 1983). But more recently also fine roots from tree species both temperate (Yamamoto et al., 1995; Dittert et al., 2006) and tropical (Barbosa and Davide, 1997; Noldt et al., 2001; de Simone et al., 2002) were investigated. The limited oxygen supply of flooded fine roots leads to inhibition of mitochondrial respiration and induces aerenchyma formation in the primary tissue to compensate for the induced exogenous stress.

Seasonal drought conditions on the other hand may initiate secondary changes in the epidermis and in hypodermal cell walls of the fine roots (Waldhoff et al., 1998; de Simone et al., 2003).

The tropical species *Ceiba pentandra* (L.) Gaertn. (sumaúma), Bombacaceae, can grow in the central Amazon both on sites with a distinct annual dry season (terra firme) as well as under seasonal inundation (várzea).

The objective of the following study of this commercially important species was to find out in how far dynamic adaptation of the growth and structure of the fine roots can contribute to that outstanding ecological amplitude. The structural study of the fine roots from trees from terra firme and várzea in different seasons in combination with a simulation of drought and inundation conditions in the greenhouse with young plants were expected to help explain the species' extensive ecological amplitude.

* Dedicated to Prof. Dr. F. Meyer in occasion of this 80th birthday.

Material and methods

Study areas

An experimental terra firme site of planted *Ceiba pentandra* (average height 13m, Ø 27 cm) was selected. The plantation is located at 28 km north of Manaus and exposed to a distinct annual drought period. The plantation (3°8' S, 59°52' W) was established in 1992 as part of the bilateral project "Studies of Human Impact on Forests and Floodplains in the Tropics" (Shift) (Feldmann et al., 1993; Lieberei and Salati, 2000) and is managed by the CPAA-EMBRAPA Amazônia Ocidental, Manaus (Fig. 1).

The effect of a seasonal inundation at a várzea site on the structural adaptation of fine roots was studied at a plantation of *Ceiba pentandra* (planted 1992, average height 23m, Ø 48 cm) of the Instituto Nacional de Pesquisas da Amazônia (INPA) in the region Costa do Caldeirão (2°53'S, 59°58 W') near the river Solimões (Fig. 2).

The annual precipitation at the experimental sites in 2004 and 2005 was about 2600 mm, the average air temperature 27.7 °C. At the terra firme site the drought period lasted from about July to November. In the várzea the high tide of flooding is around July and August (Fig. 2, arrow indicates maximum water level). The soil condition of the várzea site favours a sustainable tree growth due to the annual nutrient input by flooding. At the terra firme site the soil is a more acetic latosol and poor in macronutrients such as phosphorus, potassium and calcium (comp. Schmidt, 1996; Neves, 1999; Bauch et al., 1999). Consequently, the growth of *Ceiba pentandra* on the várzea site is superior to that on the terra firme site (Fig. 1 and 2).

Selected fine roots at the experimental areas

The experimental period at the two sites (terra firme and várzea) comprises the years 2004 and 2005. The selection of fine root series and adventitious roots (only várzea) was carried out in five repetitions each during the months October and November 2004 as well as March and April 2005. This timing allows the study of the structural development of the fine roots during the terra firme wet and dry season (Noldt, 2000) as well as the effect of the rising inundation on fine root development.

Drought and inundation experiments under greenhouse condition

For the drought and inundation experiments under controlled conditions 25 seedlings of *Ceiba pentandra* were cultivated in soil for 6 months in the tropical greenhouse of the Federal Research Center of Forestry and Forest Products, Hamburg (Fig. 3).

Subsequently the plants were then transferred into a 4 dm^3 container each, adding a mixture of mineral soil from the study plantation at

Fig. 1: Experimental terra firme site north of Manaus. Plantation (planted 1992) of *Ceiba pentandra*, CPAA-EMBRAPA Amazônia Ocidental, Manaus.

Fig. 2: Experimental várzea site in Costa do Caldeirão. Plantation (planted 1992) of *Ceiba pentandra*, Instituto Nacional de Pesquisas da Amazônia, Manaus (arrows show maximum water level during the inundation period).

Fig. 3: Culture of 6 month old seedlings of *Ceiba pentandra* in a tropical greenhouse.

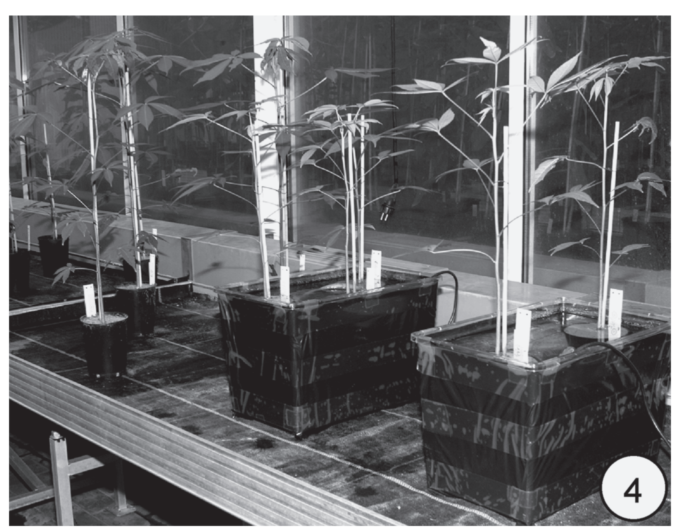

Fig. 4: Begin of the drought (left) and inundation (right) condition maintained for 16 weeks.

the terra firme near Manaus to ensure adequate mycorrhization (comp. NOLDT, 2000). The plants were then exposed for an additional 16 weeks under three different conditions:

Batch one of nine plants served as control and was supplied with 100 ml rain water per day and container, which corresponds approximately to the amount of precipitation during the wet season at the terra firme experimental site.

Batch two of eight plants was not supplied any water to study the fine root development under conditions of an extreme dry season (Fig. 4, left).

Batch three of eight plants was inundated with rain water in a 40 dm^3 container maintaining a water level of about 5 cm above the soil surface (Fig. 4, right). The control of the water circulation was maintained by a pump.

During the 16 week experimental period the height of the plants and the number of developed leaves were documented at monthly intervals. At the end of the experiment, sets of fine roots and adventitious roots were selected and the anatomical, histochemical and spectroscopic findings compared with those obtained from the fine roots collected at the terra firme and várzea study sites.

Experimental conditions in the tropical greenhouse were: relative humidity 75-80 %, air temperature 26-28 °C, day/night rhythm 12 hours, photosynthetic active radiation (PAR) around 250 µmol $m^{-2}s^{-1}$.

Light-microscopic studies

The development of the fine roots of *Ceiba pentandra* on the terra firme and várzea sites and their adaptation to the different site conditions were studied with continuously harvested sets of fine roots. For the histochemical tests, hand made sections about 8-10 µm thick were prepared according to the parafilm method (FROHLICH, 1984). The following reagents were applied:

Differentiation of lignified and unlignified cell walls was achieved by double staining with safranin and astrablue (Fig. 5).

The presence of suberization of the exodermal and endodermal cell walls was studied with sections stained for one hour in 0.1 % solution of berberine-hemisulphate, then treated for 30 min. with 0.5 % solution of aniline blue and finally transferred to 0.1 % $FeCl_3$ in order to detect suberin deposition under fluorescence light according to BRUNDRETT et al. (1988) (Fig. 6).

Cellular UV-spectroscopic analyses

The cellular UV-microscope-spectrophotometry (UMSP 80, ZEISS) is a very sensitive method for the identification of lignin within the cell wall and for the detection of synthesised secondary polymers such as suberin (NOLDT et al., 2001).

Small samples of fine roots (5 mm long) were fixed in formaldehyde-glutaraldehyde-mixture according to KARNOVSKY (1965), washed with 0.1 mol cacodylbuffer, dehydrated in acetone, and embedded in resin (SPURR, 1969). 1 µm thin sections were prepared and subjected to 1 μm^2 small point measurements. The spectra were plotted from 250 nm to 400 nm (KOCH and GRÜNWALD, 2004). In addition, UV photos at 278 nm were taken from the thin sections.

Results and discussion

Study site at the terra firme

The rapid development of new fine roots of *Ceiba pentandra* during the rainy season at the terra firme site leads to specifically adapted tissues from epidermis to exodermis, and from cortex to endodermis including the central cylinder (Fig. 5).

Both within the cortex (cor) and the central cylinder (zz) only a few small intercellular canals (black arrows) were formed. With the transition to the dry season the outer epidermis cell walls increased in thickness and degree of lignification. The lignin was identified histochemically under fluorescence light (BRUNDRETT et al., 1988) (Fig. 6) and with cellular UV-spectrometry (Fig. 10). The lignin content of the wall of primary xylem cells also increased. Moreover, fluorescence reveals a suberization (yellow arrows) in the tangential walls of the exodermis (ex) and in the radial walls of the endodermis (en). With the beginning of the dry season at the same terra firme site, *Carapa guianensis* and *Swietenia macrophylla* (Meliaceae) also developed wall thickenings within the the exodermis including a suberin lamella and a high lignin content in the primary xylem (NOLDT et al., 2001). This adaptation to a dry season directs the restricted uptake of ions into the fine root system and controls the release of ions into the soil (PETERSON, 1988). Moreover, both species of the Meliaceae and *Ceiba pentandra* show a cambium dormancy during periods of soil dryness (DÜNISCH et al., 2002; DE AZEVEDO, unpubl.). The deficiency particularly of macronutrients (K, Ca, P) on terra firme leads to slower growth compared to the situation in the várzea (NEVES, 1999).

In this context, it was observed that wood density along the gradient pith to cambium of the terra firme plantation trees with moderate growth is significantly superior to that of the trees grown on the várzea site, which can be explained with a lower portion of vessels in the xylem (DE AZEVEDO et al., 1998).

Study site at the várzea

Microscopic studies of fine roots from the seasonally inundated várzea site showed as the most striking alteration lysigenously developed extensive aerenchyma within the cortex (Fig. 7). This phenomenon indicates the adaptation to oxygen deficiency as described in a rewiew article by KREUZWIESER et al. (2004). Since oxygen is essential for mitochondrial respiration, this process cannot be maintained under anoxic conditions and will be replaced occasionally by other pathways. The structural alterations and adaptations such as the development of a lysigenous intercellular system contributes to sustainable photosynthesis and growth. The significance of that lysigenous aerenchyma for the processes of plant ventilation in relation to soil flooding and submergence was described in detail by JACKSON and ARMSTRONG (1999).

The cambial activity is maintained, apparently even during the inundation period as opposed to the dormancy observed in terra firme trees during a distinct dry period (DE AZEVEDO, unpubl.). However, WORBES (1985, 1997) demonstrated for other várzea species a cambial dormancy during long-term flooding.

A special survival strategy of *Ceiba pentandra* at the seasonally inundated várzea is the formation of many adventitious roots which develop above the soil surface (Fig. 11). The cortex of these adventigious roots reveals isodiametric cells with only very small intercellulars. The epidermis does not lignify and the exodermis cell layer lacks suberization (Fig. 8a) opposed to the fine root structure which occurs on terra firme sites (Fig. 6). Within the central cylinder the lignin content of the cell walls in the primary xylem (Fig. 8b) of the adventigious roots corresponds to that in the fine roots at the sites of the terra firme (Fig. 6).

The strategy of *Ceiba pentandra* forming adventitious roots depends on the special antagonistic role of cytokinin and auxin. ALONI et al. (2006) showed that auxin promotes the formation of lateral fine roots as well as adventitious roots. In addition, during flooding ethylene production favours adventitious root formation (YAMAMOTO et al., 1995).

Simulation of growth conditions on the terra firme and in the várzea

The simulation of growth conditions for *Ceiba pentandra* on the terra firme and várzea in a tropical greenhouse offers the possibility to

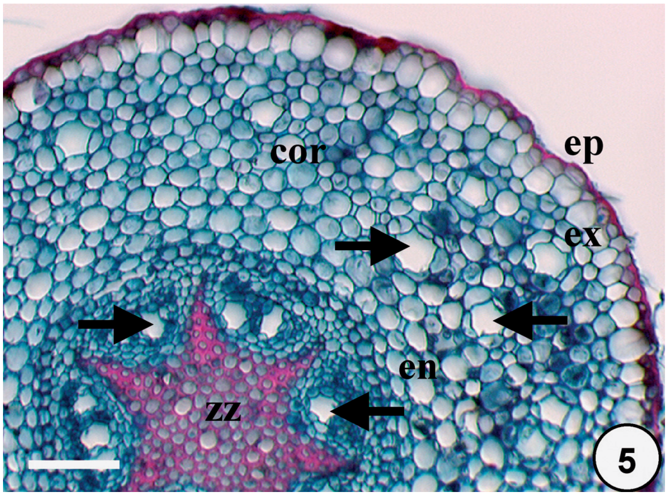

Fig. 5: Transverse section of a fine root 3 cm from the tip, harvested during the wet season on the terra firme site. ep = epidermis, ex = exodermis, cor = cortex, en = endodermis, zz = central cylinder; black arrows indicate small intercellular canals. Double staining with safranin/astrablue. Bar = 100 µm.

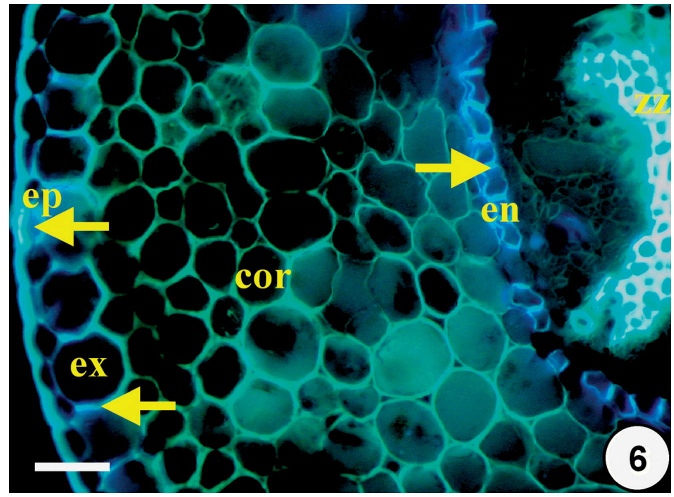

Fig. 6: Transverse section of a fine root harvested during the dry season on the terra firme (fluorescence light). The outer epidermis (ep) cell wall increased in thickness and lignification. Suberin formation (yellow arrows) in the tangential walls of exodermis (ex) and radial walls of endodermis (en) contributes to prevent dessication of the roots. Bar = 50 µm.

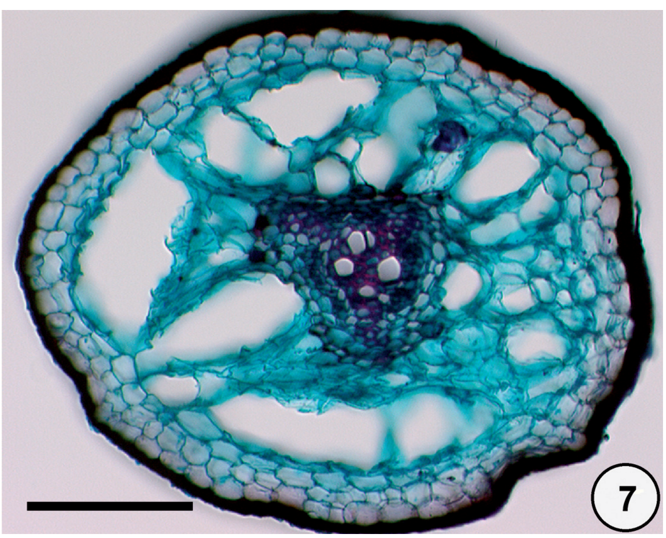

Fig. 7: Transverse section of a fine root with a pronounced intercellular system formed lysigenously in the cortex during the inundation period. Bar = 300 µm.

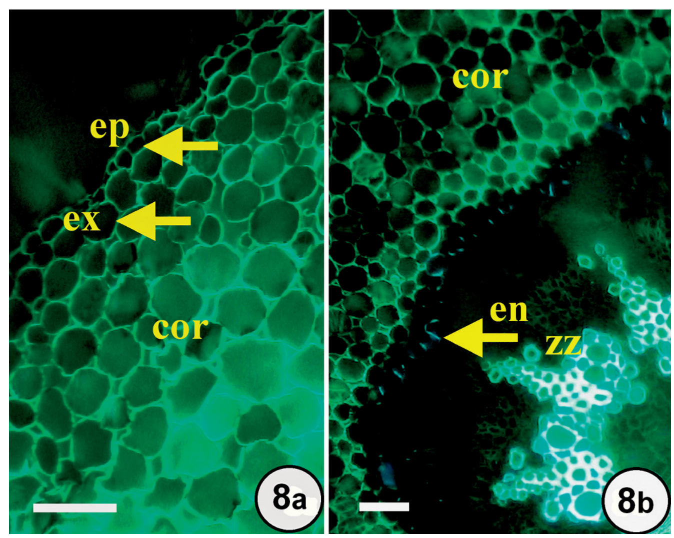

Fig. 8a: Transverse section of an adventitious root (3 cm from the root tip) with thin walled and unlignified isodiametric cortex cells (cor) with only small intercellular spaces (fluorescence light). Bar = 50 µm.

Fig. 8b: Inner part of the transverse section from Fig. 8a. Within the central cylinder (zz) only the primary xylem reveals distinct lignification. Bar = 50 µm.

continuously observe the growth dynamics and the development of the fine roots as well as adventitious roots of young plants. Six month old plants (Fig. 3) were separated into three series to grow for an additional 16 weeks as controls, under dry conditions and under inundation, respectively. During this period the height of the plants and the number of developed leaves were recorded (Fig. 9). The control plants (normal conditions) grew well during the 16 weeks and reached a height of 76 ± 15,2 cm with 19 ± 4 leaves. The plants under inundation condition showed nearly identical growth and leaf formation (height 77 ± 13,4 cm, 17 ± 3 leaves). This congruence in growth can be explained by the nearly equal photosynthesis performance shown by inundated plants and controls (Noldt and Kriebitzsch, unpubl.). Under dry conditions the plants responded already after five weeks with a distinct reduction in height increment and, after another four weeks, height growth and the cambial activity ceased. Starting from an average of about 30 cm, the final height was 47 ± 6,6 cm, the number of leaves 8 ± 2: during the experimental period some leaves were lost while a few new ones were formed. The 25 plants did not shed their leaves, a possible survival strategy under drought and adverse inundation conditions, which Waldhoff et al. (1998) explained with shade-tolerance based on their respective study under controlled conditions.

Of main interest was the continuous anatomical and histochemical study of the development and adaptation of the fine roots. The greenhouse experiments with the plants grown under the control and dry conditions confirmed the structural adaptation of the fine roots

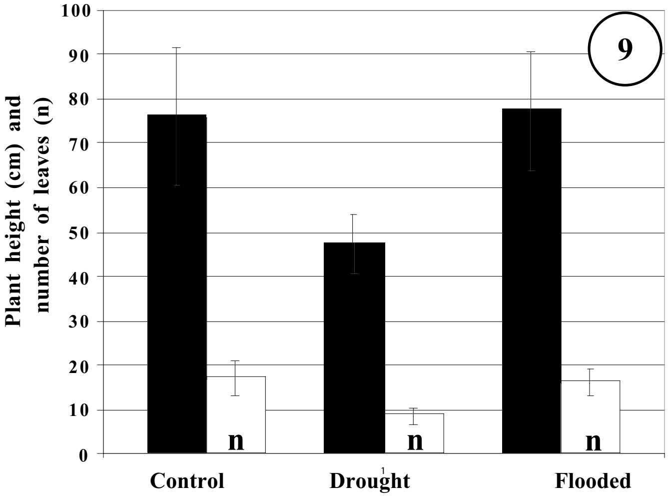

Fig. 9: Growth of *Ceiba* plants in a tropical greenhouse. After 6 months normal plant growth, three batches were subjected in three to different conditions (control, drought and flooded) for 16 weeks. Final plant height and number of leaves were documented.

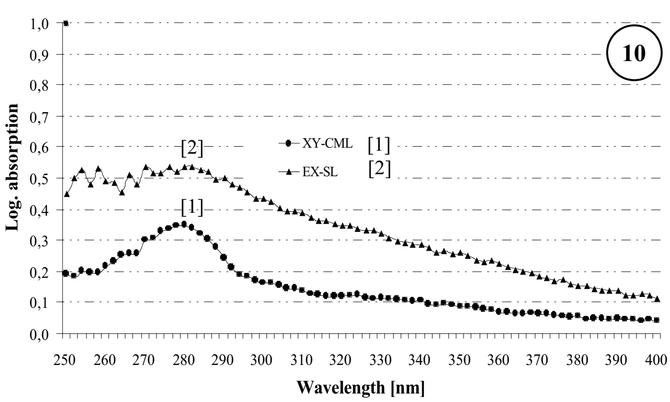

Fig. 10: Cellular UV-spectra of the exodermis cell wall and primary xylem of fine roots from the terra firme site. [1] Control: primary xylem; [2] Dry season: exodermis with suberin lamella, distinct increase in wall thickness and degree of lignification.

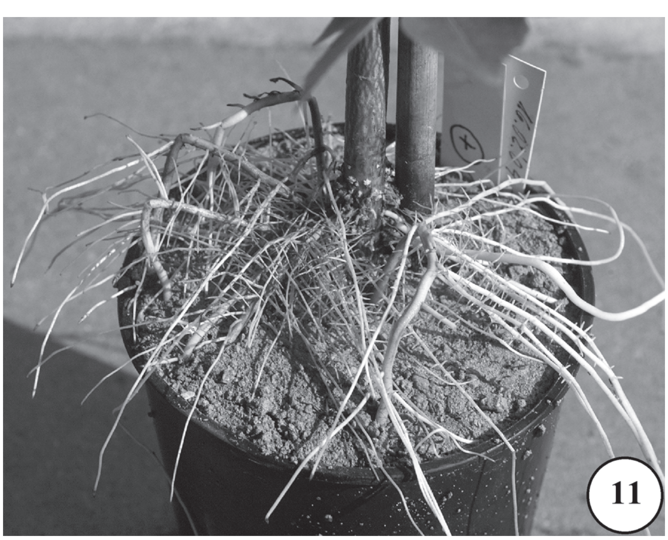

Fig. 11: *Ceiba pentandra* plants in the tropical greenhouse after 8 weeks of inundation (comp. Fig. 4) with adventitious roots above soil surface.

as observed under the wet and dry season on the terra firme. With increasing soil dryness the cell walls of the lignified epidermis became thicker, the exodermis suberized.
UV-spectroscopic analyses of the subcellular individual wall layers support the findings of the anatomical and histochemical studies and reveal a specific UV spectrum of the thin suberin lamella in the exodermis cells of fine roots from plants grown under dry conditions (Fig. 10 [2]). A secondary formed suberin lamella within the tangential cell wall of the exodermis is obviously a response to stress. Liese and Weiner (1997) could demonstrate this phenomenon after wounding in bamboo culms. Suberization acts as a protective mechanism against dessication. UV-spectroscopic point analyses of the compound middle lamella (CML) of the primary xylem show a typical spectrum with an absorption maximum at 278 nm wavelength and a shallow minimum at about 255 nm, specific for hardwood lignin (Fig. 10 [1]).
The fine roots of the flooded plants under greenhouse conditions formed lysigenous aerenchyma corresponding to the inundation season in the varzea.
The vigorous development of adventitious roots (Fig. 11) under simulated inundation conditions in the tropical greenhouse corroborates the response strategy of *Ceiba* trees under inundation in the várzea. The initiation of adventitious roots started already a few days after inundation and Fig. 11 demonstrates the status after 8 weeks. De Simone et al. (2002) emphasize on the basis of their adaptation study under greenhouse condition with six tree species typical of the Amazon floodplain that only two species (*Salix martiana*, *Tabernaemontana juruana*) were in the position to develop adventitious roots. In both species the cortex cells, which are not lignified showed only small intercellular spaces between them, characteristic also for the adventitious roots of *Ceiba pentandra*.

Conclusion

The experiments in the tropical greenhouse contribute to explain the structural and physiological adaptation of *Ceiba pentandra* to various terra firme and várzea site conditions.
There is no doubt that the commercial demand for wood of *Ceiba pentandra* will increase significantly in the national Brazilian and the international markets. Therefore, the extreme adaptability of this species to different growth conditions is a good reason to favour it in plantations and enrichment systems of the várzea. Junk (2000) emphasizes the practical concept for the sustainable use of várzea resources and proposes several possibilities to also include the aspect of wood production on the long-term basis. The experience of Parolin (2000) with the commercial use of trees from floodplains also encourages the cultivation of *Ceiba pentandra*. The experimental plots at the terra firme are testimony to its capacity of adapting to the site resulting in formidable tree growth and wood production (De Azevedo et al., 1998).

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