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ADAPTATIONS TO FLOODING BY TROPICAL TREES: MORPHOLOGICAL AND ANATOMICAL MODIFICATIONS

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Resumo:

“Adaptações de espécies arbóreas tropicais ao alagamento: modificações morfológicas e anatômicas.”

Muitas das comunidades inundáveis estão nas regiões tropicais e são ricas em espécies arbóreas. Pouco se sabe sobre os mecanismos de tolerância ao alagamento que estas espécies desenvolveram. Entretanto, os estudos têm mostrado que tanto adaptações metabólicas como morfológicas e anatômicas são importantes para possibilitar a sobrevivência dessas plantas em condições hipóxicas. Dentre as modificações morfológicas e anatômicas provocadas pelo alagamento, destacam-se a hipertrofia de lenticelas, a formação de aerênquimas, a hipertrofia de caules e o enraizamento adventício. A principal função destas modificações parece estar relacionada a uma maior oxigenação das raízes submersas, permitindo a manutenção de uma produção energética satisfatória. O etileno, que tem seus níveis aumentados nas plantas por causa do alagamento, parece ser o principal hormônio envolvido com o aparecimento destas modificações morfológicas. Apenas no caso da origem e desenvolvimento das raízes adventícias é que tem sido sugerido um sinergismo entre etileno e auxinas. Em decorrência da complexidade de respostas que as espécies arbóreas tropicais apresentam quando inundadas, surge a necessidade de ampliarmos os estudos para melhor entendermos estas questões.

Abstract:

Many plant communities subjected to flooding are found in tropical regions and are rich in tree species. Little is known about the flood-tolerance mechanisms these species have developed. However, studies have shown that metabolic, morphological and anatomical adaptations are all important for the survival of these plants in oxygen-deficient conditions. Lenticel hypertrophy, aerenchyma formation, stem hypertrophy and the formation of adventitious roots are among the morphological and anatomical adaptations caused by flooding. These modifications enhance the oxygenization of submerged roots, permitting sufficient energy production for survival. Ethylene, which increases markedly in flooded plants, seems to be the main hormone involved in bringing about these morphological modifications. In the case of the initiation and development of adventitious roots there is a synergism between ethylene and auxin. Broader studies are now necessary to improve the understanding of these questions because of the complexity of the responses of tropical tree species to flooding.

Introduction

Many naturally flooded plant communities occur in the tropical regions, but little is known about the mechanisms that permit species to survive these conditions (Joly & Crawford, 1982). Many of these communities are important for forest regeneration since they are rich in tree species. However, responses to flooding by trees are complex and may vary with the age or part of the plant. These variables may be attributed to hormonal factors (Rinne, 1990).

According to Broadfoot (1967), plant response to water saturation of the soil varies with the growth phase. When the plant is dormant, resistance is high but before or during rapid growth phases damage is more severe. Response mechanisms have mainly been studied in temperate, herbaceous species. Flooding occurs in the winter in temperate regions, a period of low metabolic activity. This is unlike tropical regions where flooding happens in the summer, when the plants have a high metabolic rate and are growing fast. This will obviously produce more complex flood-tolerance mechanisms in tropical trees compared to their temperate counterparts (Joly, 1991).

Flooding leads to a series of physico-chemical and biological processes which profoundly influence the quality of the soil as a development medium for the plants. Ponnampertuma (1984) reported that flooding decreases gas exchange between the soil and the atmosphere because oxygen diffuses more slowly in water than in air. The oxygen contained in the soil is rapidly consumed by micro-organisms and roots, while gases such as nitrogen, carbon dioxide, hydrogen and ammonia, among others, are formed by soil metabolism and entrapped in the wet soil. The environment becomes anaerobic, giving rise to a stress situation for the roots; plants respond to this condition with greater or lesser efficiency, and are described as tolerant, apparently tolerant and intolerant species.

Jackson (1993) suggested that changes in the flow of substances between roots and shoot can mediate shoot responses to stress imposed on the roots by flooding. "Positive", "negative", "accumulative" and "debit" messages may be involved. For example, alterations in the hormone levels, hormone precursors and other solutes in the sap of the xylem caused by hypoxia may constitute active physiological messages, modifying the physiology and development of the shoot (Jackson & Campbell, 1975b; Bradford & Yang, 1980; Davies *et al.*, 1994; Else *et al.*, 1995). Thus, the survival of many plant species under flood conditions may be improved by the functions exercised by morphological and anatomical modifications caused by these messages. The present review describes these modifications and discusses their importance and origin, emphasizing data obtained from tropical trees.

Lenticel hypertrophy

Lenticel hypertrophy occurs in various woody species subject to flooding (Kawase, 1981a; Andersen *et al.*, 1984; Kozlowski, 1984) and it is suggested that it

enhances internal oxygen diffusion to submersed roots (Kozłowski, 1984) by acting as entry sites for atmospheric oxygen. According to Reid & Bradford (1984), this oxygen diffusion re-establishes the semi-permeability of membranes and consequently maintains water uptake and other membrane-based processes. In describing the responses of *Chorisia speciosa*, Joly (1991) suggested that these structures play a double role in this species, by markedly improving root aeration but also liberating potentially toxic products such as ethanol, acetaldehyde and/or ethylene into the environment, which may accumulate as a consequence of flooding. Tsukahara & Kozłowski (1985) suggested the same in the light of their work with *Platanus occidentalis*.

The role of hypertrophic lenticels in gas exchange was confirmed in *Pinus contorta* (Philipson & Coutts, 1980), *P. clausa*, *P. serotina* and *P. taeda* (Topa & McLeod, 1986). *P. silvestris* develops many hypertrophic lenticels (Aronen & Häggman, 1994). The authors suggested that even though this species is not tolerant of flooding, lenticels do contribute to the tolerance of other species that thrive in wet localities.

Tropical species which show lenticel hypertrophy when flooded include *Cedrela fissilis* (Lobo, 1990; Marques *et al.*, 1996) *Chorisia speciosa* (Joly, 1994; Giloni, 1995), *Inga affinis* (Lieberg, 1990), *Peltophorum dubium* (Joly, 1982; Medri *et al.*, 1998), *Schyzolobium parahyba*, *Pseudobombax marginatum*, *Enterolobium contortisiliquum*, *Anadenanthera colubrina*, *A. peregrina* and *A. falcata* (Joly, 1982). In *Sesbania virgata*, a tolerant species (Davanso, 1994), and in *Jacaranda puberula*, an intolerant species (Pimenta *et al.*, 1996), there was no lenticel hypertrophy, but deep cortical cracks could be playing the same role as hypertrophic lenticels with different degrees of efficiency.

Indices of hypertrophic lenticel production in relation to survival of flooding have been generated for tropical trees. Conspicuous lenticel hypertrophy was observed during flooding in *Sebastiania commersoniana* (Fig. 1), a species characteristic of regions subjected to flooding which may form 60-80% of the continuous strata of gallery forest. From studies of aerobic respiration of the roots after up to 60 days of flooding, it is apparent that these structures are important for the survival of this species during long periods of flooding (Fig. 2). This period was sufficient for considerable lenticel hypertrophy and moderate formation of adventitious roots.

The importance of hypertrophic lenticels for oxygen diffusion in submersed roots was tested experimentally in two species. After a short period of flooding there was a great decrease in aerobic respiration in *Cedrela fissilis* (Fig. 3). After 60 days flooding, however, this low aerobic respiration remained only in those plants where the hypertrophic lenticel had been sealed with lanolin grease. In plants where the lenticels were not sealed, aerobic respiration reached levels as high as those in plants growing in well drained soils. This importance of hypertrophic lenticels was also indicated in experiments with *Peltophorum dubium*, in which oxygen uptake by the roots from nutrient

solution was measured at different external oxygen concentrations (Fig. 4). When the many hypertrophic lenticels of this species were sealed with lanolin, there was an increase in the oxygen uptake from the nutritive solution, indicating that prior to applying the lanolin, lenticels were a source of oxygen for the roots. These results agree with those of Joly (1994) working with *Chorisia speciosa* and with Lobo and Joly (1995), working with *Talauma ovata*, a characteristic species of swamp forests.

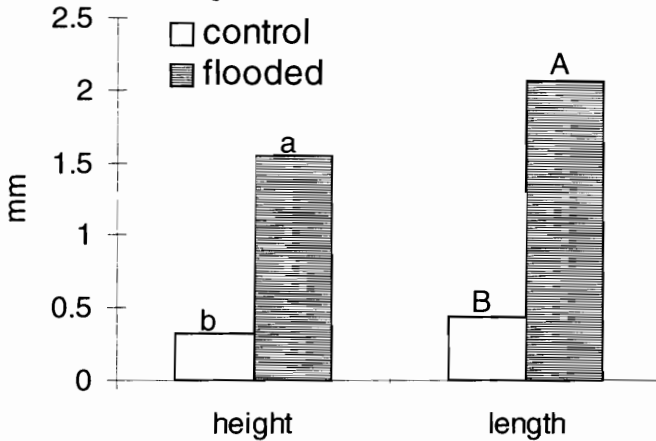


Fig. 1. Size of *Sebastiania commersoniana* main root lenticels. Bars followed by different capital or lower-case letters differ statistically by the Tukey Test ($P < 0.05$). Taken from Kolb (1995).

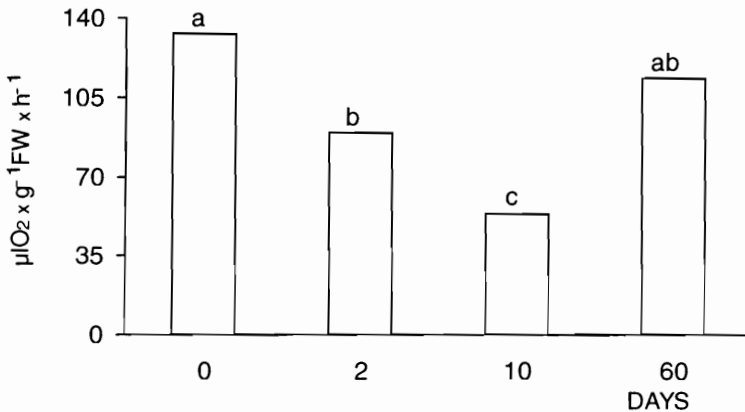


Fig. 2. Oxygen uptake by roots of *Sebastiania commersoniana*, after 0, 2, 10 or 60 days of flooding. Bars followed by same letters do not differ statistically by the Tukey Test ($P < 0.05$). Taken from Rogge (1995).

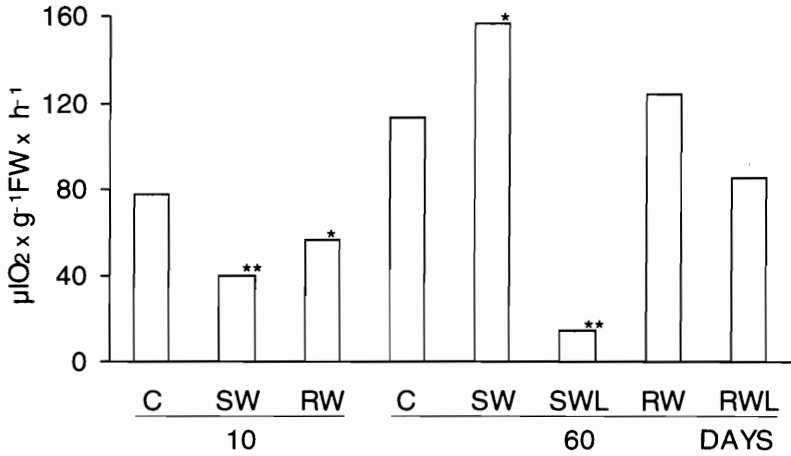


Fig. 3. Oxygen uptake by roots of *Cedrela fissilis* after 10 and 60 days flooding and submitted to different treatments. C-control; SW- still water; RW-running water; SWL-still water with sealed lenticels; RWL-running water with sealed lenticels. * $P < 0.05$; ** $P < 0.01$. Taken from Marques *et al.* (1996).

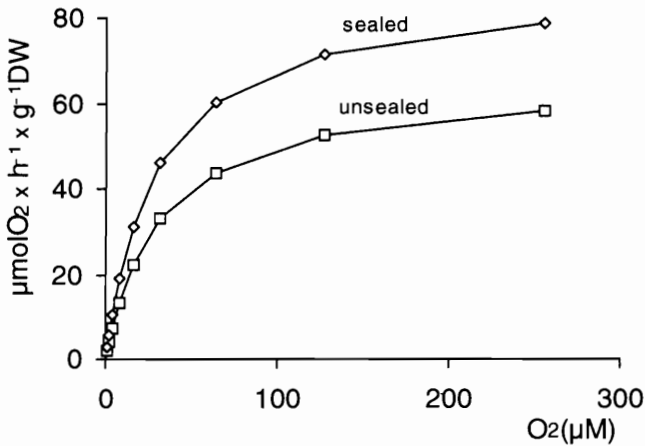


Fig. 4. Rate of oxygen uptake from nutrient solution by roots of *Peltophorum dubium*, cultivated under hypoxic conditions with lenticels sealed with lanolin grease or left open (unsealed) to the atmosphere.

There was extensive lenticel hypertrophy in *Mangifera indica* stems which survived flooding; where no hypertrophy was observed, plants did not survive (Larson *et al.*, 1991). The same authors reported that when the hypertrophic lenticels were sealed, flooded plants died within three days. *Cedrela fissilis*, *Peltophorum dubium* and *Chorisia speciosa* are woody species which do not occur in regions subjected to flooding despite forming lenticels readily when flooded experimentally. This agrees with Larson *et al.* (1991) who point out that hypertrophic lenticels alone do not confer tolerance to flooding. Andersen *et al.* (1984) also observed lenticel hypertrophy in submersed stems of *Prunus persica*, a species intolerant of flooding.

Ethylene is the probable cause of hypertrophy of lenticels and also of the stem base (Kawase, 1981b). This effect has been connected with the increase in the activity of β (1,4) glucanase (cellulase) which possibly weakens the wall, thus favouring cell expansion (Kawase, 1979). Thus, the plant needs morphological and/or metabolic adaptations to survive flooding and these are often mediated by plant hormones, most notably ethylene (Jackson, 1985; Voesenek *et al.*, 1992).

Since it was shown that flooding causes an increase in the level of ethylene in plants (Kawase, 1972) and that the symptoms caused by flooding are similar to those caused by ethylene, it has been suggested that this hormone may be responsible for some of the morphological responses to flooding (Kawase, 1974; Jackson & Campbell, 1975a). The biochemical and physiological pathway for ethylene production induced by flooding was clarified by Bradford & Yang (1980). Under low oxygen tension, roots accumulate ACC (1-aminocyclopropane-1-carboxylic acid), a precursor of ethylene because of the arrest of ACC oxidation to ethylene and possibly an increase in ACC synthase activity. This ACC is then transported, via xylem, to aerial parts, where it is rapidly converted to ethylene by the enzyme ACC oxidase. The increased activity of this enzyme in tomato shoots submitted to these conditions (English *et al.*, 1995) confirmed that the activity of ACC oxidase in the leaves is induced by anaerobiosis in the roots. The molecular base of the increase in ACC synthase in oxygen deficient roots (Wang & Arteca, 1992) is not clear but may include enhanced transcription of ACC synthase genes (Olson *et al.*, 1995). Four different ACC synthase genes have been described in tomatoes.

Larson *et al.* (1993) observed that in *Mangifera indica*, low oxygen concentrations and/or the application of ethylene increased hypertrophy in lenticels, and 100% oxygen decreased hypertrophy. These same authors also observed that there was no increase in the ethylene concentration in a treatment with low oxygen concentration, but there was lenticel hypertrophy. They suggested that the hypertrophy is, in part, a phenomenon of tissue or cell hydration not mediated by this hormone, and that both the endogenous level and the exogenous application only increase the hypertrophic response. However, they concluded that hypertrophic lenticels associated with other morphological responses of adaptive importance are, at least in part, mediated by ethylene.

Aerenchyma formation

The aerenchyma is a gas transporting tissue and an oxygen reservoir. It allows aerobic respiration to proceed in tissues without direct access to oxygen from the air (Esau, 1976). Many plants able to resist soil hypoxia develop aerenchyma but sometimes this tissue is not functional. The formation of aerenchyma reduces both the relative quantity of respiring tissue (thereby decreasing total oxygen requirement for the root) and internal resistance to oxygen diffusion. Overall aeration of the roots and rhizosphere is enhanced (Armstrong, 1979; Drew *et al.*, 1985). Rhizosphere oxidation itself is an important component of flood tolerance (Ottow *et al.*, 1982) because by these mechanisms, potential soil toxins, especially chemically reduced forms of Fe, Mn and H₂S, can be immobilized and detoxified (Armstrong, 1979; Ottow *et al.*, 1982; Laan *et al.*, 1991).

Aerenchyma may form by schizogeny or lysigeny. In flood-tolerant plants, schizogenic aerenchyma extends almost to the root tip, unlike lysigenous aerenchyma, which develops secondarily in differentiated cortical tissues (Konings, 1983).

Many flood-intolerant plants have low root porosity when growing under adequate external aeration, but may form roots with greater porosity when aeration is impeded (Drew, 1990). Increased porosity normally develops by cortical cell lysis in young roots at some distance from the tip. As a consequence, oxygen diffusion is greatly enhanced. There may also be associated changes to surviving cells that inhibit radial oxygen loss from the basal region, allowing more oxygen to be transported to the root tip (De Willingen & Van Noordwijk, 1989).

Pezeshki *et al.* (1993) reported that for *Spartina patens*, a species which grows in flooded soils, an internal oxygen diffusion system from the aerial part to the roots is essential for survival during long hypoxic periods. These authors stated that in this species cortical aerenchyma can form near the root tip. This has also been observed in *Eriophorum angustifolium* where the air spaces are absent only from the three cell layers between the junction of the root cap and pro-meristem (Gaynard & Armstrong, 1987). Furthermore, Clark & Harris (1981) say that the presence of suberized and lignified cell layers beneath the epidermis presumably decreases permeability to oxygen, easing its diffusion to the tip. These anatomical aspects are less developed or absent in plants which are intolerant of flooding (Armstrong, 1979).

Several tropical tree species have shown enhanced aerenchyma formation in the stems when flooded: *Jacaranda puberula* (Pimenta *et al.*, 1996), *Spathodea campanulata* (Medri & Correa, 1985) and *Peltophorum dubium* (Medri *et al.*, 1998). However, *Sesbania virgata*, a species of regions subject to extensive flooding, had the most conspicuous intercellular air spaces in the stem base (Davanso, 1994). In flooded *Chorisia speciosa*, *Schyzolobium parahyba* (Joly, 1982), *Talauma ovata* (Lobo & Joly, 1995) and *Sebastiania commersoniana* (Kolb, 1995), root porosity in the original roots was similar to that of the roots of the control plants. However, these species produced new superficial roots and/or adventitious roots which were highly porous.

The development of aerenchyma in plants after flooding along with the hypertrophic lenticels is attributed to the increase in the ethylene level. In roots of flooded maize, ethylene is the principal agent inducing aerenchyma (reviewed in Jackson, 1989). Kawase (1981b) suggested that ethylene increases the activity of the cellulases and this is related to the development of aerenchyma in herbaceous plants (He *et al.*, 1994). Topa & McLeod (1987) have suggested that ethylene promotes intercellular air spaces in the roots of a temperate woody species (*Pinus serotina*) and Yamamoto *et al.* (1995), working with *Alnus japonica* seedlings, also suggested that ethylene is essential for aerenchyma and adventitious roots to develop in this species when it is flooded.

The formation of aerenchyma in flooded plants is often associated with hypertrophy of the stem base. This has frequently been observed in studies of flooded plants (Wample & Reid, 1979, Blake & Reid, 1981; Yamamoto & Kozlowski, 1987). There is little evidence to substantiate increased cambial activity or accelerated wood production as the cause of hypertrophic stems in flooded woody plants (Yamamoto *et al.*, 1995). However, unpublished data of these authors suggests that in *Fraxinus mandshurica* seedlings, stem hypertrophy may be due, in part, to an increase in number and diameter of woody fibers. Data from xylem studies in tropical tree species which had stem hypertrophy when flooded, such as *Chorisia speciosa* (Giloni, 1995) and *Sebastiania commersoniana* (Kolb, 1995), showed no difference from unflooded control plants. There is a question of whether stem hypertrophy is essential for flooding tolerance in woody trees (Larson *et al.*, 1991). Certainly by itself it does not necessarily confer tolerance since it is seen in intolerant species, for example in *Jacaranda puberula* (Table 1), while no hypertrophy develops in flood-tolerant species (Joly, 1982) including *Campomanesia xanthocarpa* (Table 2).

Adventitious rooting

Many flood-intolerant species lose part of the original root system through decomposition and do not regenerate new roots. This regeneration is more frequently observed in tolerant species that form new roots from the original root system, or from the stem (adventitious roots) or from both (Kozlowski, 1984), for example, *Alnus japonica* (Yamamoto *et al.*, 1995).

Tsukahara and Kozlowski (1985) studied the importance of adventitious roots in *Platanus occidentalis*, and found that when flood-induced adventitious roots were removed, shoot growth was depressed. The relative tolerance of three *Eucalyptus* species was also correlated with differences in adventitious root production. However, work with *Alnus glutinosa* (Gill, 1975), *Acer rubrum* and *Betula nigra* (Tripepi & Mitchell, 1984) suggests that adventitious roots are not important for the survival of these species when flooded.

Table 1: Diameter of stem base of *Jacaranda puberula* plants flooded for up to 60 days. Means followed by the same letter between treatments were not statistically different by the Tukey Test ($P < 0.05$).

Days of treatment	Diameter of stem base (mm)	
	control	flooded
0	6.12 a	6.40 a
10	6.66 a	7.11 a
20	7.01 a	8.18 a
30	8.15 b	12.68 a
40	8.83 b	13.88 a
50	8.78 b	14.02 a
60	9.22 b	14.67 a

Table 2: Diameter of stem base of *Campomanesia xanthocarpa* plants flooded for up to 60 days. Means followed by the same letter between treatments were not statistically different by the Tukey Test ($P < 0.05$).

Days of treatment	Diameter of stem base (mm)	
	control	flooded
0	2.64 a	2.48 a
15	3.12 a	2.90 a
30	3.39 a	2.63 a
45	3.75 a	2.95 a
60	4.36 a	3.13 b

Evidence of the physiological importance of adventitious roots in providing some degree of flood-tolerance in woody plants was put forward by Tsukahara & Kozlowski (1985). These authors claim that such roots increase the water and nutrient uptake capacity in flood-tolerant plants, thus compensating for the loss of absorption capacity due to decomposition in the original root system. Furthermore, increased adventitious root production in flooded plants is closely correlated in time with stomatal re-opening. Flood-induced adventitious roots also play an important role in the oxidation of the rhizosphere of tolerant plants. Tsukahara & Kozlowski (1985) further report that adventitious roots increase the availability of growth regulators synthesized in the roots for the benefit of the aerial part, especially gibberellins and cytokinins. For example, compared to the quantity of adventitious roots shown by *Malus domestica* after 40 days of flooding (Armstrong *et al.*, 1994), this response has not been so marked in the majority of tropical tree species studied. However, some response was observed in *Cedrela fissilis* (Marques *et al.*, 1996), *Chorisia speciosa* (Joly, 1982; Giloni, 1995) *Inga affinis* (Lieberg, 1990), *Schyzolobium parahyba*, *Anadenanthera colubrina*, *A. peregrina* and *A. falcata* (Joly, 1982) and *Talauma ovata* (Lobo & Joly, 1995) which also develop diageotropic roots. Davanso (1994) observed a high frequency of *Sesbania virgata* plants with many adventitious roots in the field in a periodically flooded locality.

Peltophorum dubium (Joly, 1982; Medri *et al.*, 1998), *Magonia pubescens*, *Kielmeyera coriacea* (Joly, 1982) and *Jacaranda puberula* (Pimenta *et al.*, 1996) did not develop adventitious roots after flooding. Kolb (1995) observed the appearance of adventitious roots in *Sebastiania commersoniana* (synonym: *S. klotzchiana*), although the effect was less marked than for hypertrophy in lenticels, in contrast to the result obtained by Joly (1994). It is possible that these different responses are due to the length of flooding. Joly (1994) flooded the plants for one month, whereas Kolb (1995) flooded the plants for twice this time.

Several studies have indicated that ethylene stimulates the formation of adventitious roots (Kawase, 1972; Riov & Yang, 1989; Liu *et al.*, 1990). Riov & Yang (1989) suggested that the promoting effect of indole butyric acid application on adventitious root formation in *Vigna radiata* was associated with the induction of ethylene biosynthesis. Yamamoto *et al.* (1995) reported that the application of AOA (amino-oxyacetic acid, an inhibitor of ACC synthesis) to *Fraxinus mandshurica* roots cultivated in anaerobic conditions strongly inhibited the formation of adventitious roots, suggesting the necessity of ethylene for adventitious rooting. However, in the absence of a reversibility test using ACC to counteract AOA, this result is unreliable.

Flooding may increase auxin levels due to the fall in IAA-oxidase activity. An increase in auxin may also contribute to the ethylene increase (Yu & Yang, 1979). Reid *et al.* (1991) suggested that the increase in ethylene at the stem base induced by flooding may cause an accumulation of IAA in the adventitious rooting zone, and this IAA may be responsible for the initiation of roots. Yamamoto & Kozlowski (1987)

reported that blockage of the basipetal transport of auxins with the application of NPA (1-N-naphthylphthalamic acid) reduced the formation of adventitious roots in *Acer negundo* seedlings despite the presence of a large quantity of ethylene. This suggests that the auxins play a major role in the regulation of adventitious root formation and that ethylene does not have a direct role. Visser *et al.* (1995) concluded that in species of *Rumex* flooding inhibited auxin transport, which accumulated at the stem base. The authors suggested that this accumulation stimulated adventitious root formation to a greater or lesser degree, depending on the sensitivity of the species to flooding. They further considered that flooding would increase the ethylene level, which would enhance the sensitivity of the tissues at the stem base to auxins, and this would then enhance the formation of adventitious roots.

Although both auxins and ethylene may be important regulatory factors in adventitious rooting of flooded plants, little information is available on how these hormones interact to influence the formation of adventitious roots. This is in agreement with Armstrong *et al.* (1994) who concluded that adventitious root formation is a much more complex process than lenticel hypertrophy and its regulation remains poorly understood.

Stomatal closure

Kozlowski (1984) suggested that there is a rapid reduction in transpiration after the onset of flooding, which may or may not be accompanied by a short period of water deficiency in the plant. This slowing of transpiration is the result of the closure of the stomata (Jackson *et al.*, 1978; Sojka & Stolzy, 1980; Dreyer *et al.*, 1991; Singh *et al.*, 1991). Singh *et al.* (1991) reported a positive correlation between stomata conductivity and water potential where the total adjustment may be attributed to the variation in water potential. However, stomata in flooded tomato plants can close in the absence of a fall in leaf water potentials (Else *et al.*, 1996).

With the exception of *Chorisia speciosa* (Table 3), which had a significant reduction in water potential during the flooding period, there was no variation in this potential in other tropical tree species studied. A decrease in water potential and, consequently, in stomatal closure, may be a response to oxygen tension in the soil, which affects membrane permeability and water uptake (Coutts, 1981). Whatever the mechanism, it also involves abscisic acid (ABA) (Jackson & Hall, 1987; Neuman & Smit, 1991), and possibly as yet unidentified anti-transpirants transported from the roots into the transpiration stream (Else *et al.*, 1996).

Pallas & Kays (1982) suggested that ethylene affects the permeability of the guard cell membranes, thus affecting stomatal closure. However, tomato plants treated with this phytohormone did not show variations in stomatal movement (Bradford, 1983).

Stomatal closure due to flooding may also be promoted by a fall in cytokinin levels which are synthesized in the roots. This is suggested because the application of

cytokinins in some species increased the stomatal opening (Selman & Sandana, 1972; Blackman & Davies, 1985). However, Neuman *et al.* (1990) did not obtain the same results with the application of cytokinins in plants with stomata closed due to flooding, and overall the results are not convincing on this point (Jackson, 1993).

Table 3: Water potential in *Chorisia speciosa* leaves after 45 days of flooding (taken from Giloni, 1995). Means followed by different letters differ statistically by the Tukey Test ($P < 0.01$).

Treatment	Water potential (MPa)
Control	-0.446 b
Flooded	-0.648 a

Other modifications

Epinasty is one of the first symptoms shown by flooded herbs (Jackson & Campbell, 1975a; Bradford & Yang, 1980; Kozlowski, 1984), but there are few records for flooded trees (*e.g.*, *Betula papyrifera*, Norby & Kozlowski, 1983; and *Hevea brasiliensis*, Sena Gomes & Kozlowski, 1988). An increase in ethylene in the shoots of flooded plants is mainly responsible for epinasty (Jackson & Campbell, 1975a; Bradford & Dilley, 1978; Bradford & Yang, 1980; Kuo & Chen, 1980; English *et al.*, 1995). Several studies have shown that the application of ethylene inhibitors such as aminoethoxyvinylglycine - AVG (Bradford *et al.*, 1982), cobalt chloride (Bradford *et al.*, 1982; Pimenta *et al.*, 1994) or silver nitrate (Bradford & Dilley, 1978) cause a decrease in the epinastic response in flooded plants.

Other common responses in flooded plants are senescence and leaf abscission (Reid & Bradford, 1984). These responses have also been observed in tropical trees such as *Cedrela fissilis* (Marques *et al.*, 1996), *Jacaranda puberula* (Pimenta *et al.*, 1996) *Sebastiania commersoniana* (Kolb, 1995), *Chorisia speciosa* (Giloni, 1995) and *Peltophorum dubium* (Medri *et al.*, 1998). Burrows & Carr (1969) relate leaf chlorosis to a reduction in cytokinin flow from the roots to the aerial parts in the xylem sap. Thus, it was suggested that leaf senescence in flooded plants may be a response to a fall in the cytokinin levels and to the increase in the levels of ethylene and abscisic acid in the foliage (Bradford & Yang, 1980; Zhang & Davies, 1986). Ethylene also appears to be involved in leaf abscission (Kozlowski, 1984). This author says that *Betula papyrifera* suffered intense abscission after 60 days of flooding, whereas the number of leaves practically doubled in the unflooded plants. Similar results had already been observed in unflooded plants with ethylene application (Jackson & Osborne, 1970).

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