

TOLERANCE TO HYPOXIA AND ANOXIA IN NEOTROPICAL TREE SPECIES

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Resumo:

“Tolerância à hipoxia e anoxia em espécies arbóreas neotropicais.”

O estresse decorrente da saturação hídrica do solo tem forte caráter seletivo. O limite às trocas gasosas do solo com a atmosfera e o rápido consumo do oxigênio presente na água por raízes e microorganismos geram hipoxia ou anoxia no solo. Isto afeta a respiração de raízes, microorganismos, e as características físico-químicas edáficas. A frequência e a duração do alagamento determinam a distribuição espacial das espécies, resultando em diferenças florísticas e fisionômicas entre, e.g., as matas de brejo, ripárias, mesófilas semidecíduas, de várzea e de igapó. A especificidade de habitat das poucas higrofilas exclusivas ou preferenciais contrasta com sua ampla distribuição geográfica. Sob hipoxia ou anoxia, a capacidade das raízes desenvolverem atividades vitais das plantas, depende da manutenção de um metabolismo respiratório, aeróbico ou anaeróbico, que gere um *pool* mínimo de nucleotídeos fosfatados e mantenha a carga energética acima do nível crítico. A diversidade de respostas morfológicas, anatômicas, fisiológicas e metabólicas à hipoxia/anoxia em plantas neotropicais, dificulta a definição de tolerância ao estresse. Estas respostas evoluíram concomitante- e complementarmente, logo, a compreensão da estratégia adaptativa de uma dada espécie sob inundação exige uma abordagem integrada, incluindo estudos de demografia e dinâmica populacional. Esta é uma revisão do estado atual do conhecimento sobre as estratégias de tolerância à inundação em plantas neotropicais.

Abstract:

The stress imposed by soil water saturation is strongly selective. Waterlogging limits gas exchange between soil and atmosphere, and in a few hours the plant roots and microorganisms consume the oxygen present in the water, causing hypoxia or anoxia. The rapid decrease in oxygen availability in the soil affects the respiratory process of roots and microorganisms, and the physical and chemical edaphic characteristics. The frequency and duration of soil saturation define the spatial distribution of species, which results in floristic and physionomic differences between, e.g., *igapó* forests, *várzea* forests, marshy scrublands, riparian forests, and semideciduous mesophilic forests. The marked habitat specificity of the few exclusively or preferentially hygrophilic species, contrasts with their wide geographic distribution. The capacity of hypoxic or anoxic roots to continue performing their vital activities depends essentially upon maintaining a minimal pool of phosphated nucleotides and an energy charge greater than the critical level. The diversity of morphological, anatomical, physiological, and biochemical responses to hypoxia/anoxia in neotropical plants poses a difficulty to the definition of stress-tolerance. These responses have evolved concomitantly and complementarily, thus, an integrative approach is needed in order to understand the adaptive strategies to flooding of a given species. This article reviews the current knowledge on flood-tolerance strategies of neotropical plants.

Introduction

Mechanisms of tolerance to water-saturated soils; evolution of the concept

The stress imposed by soil water saturation has had a strongly selective character during the course of evolution. Waterlogging eliminates soil air spaces, limiting exchange of gases with the atmosphere, and in a few hours the plant roots and microorganisms consume the oxygen present in the water, forming an hypoxic or anoxic environment.

Generally, because oxygen diffuses quite slowly in the aqueous medium, only a few millimeters of surface area suffices to maintain an aerobic environment. Much information regarding tolerance to waterlogging or flooding has been accumulated through studies on plant species cultivated for agriculture, mainly in temperate regions. In the tropics, the few studies along this line are restricted to tree species, since one of the environments most subject to natural inundation is the gallery forest. In recent times, gallery forests have been subject to strong human pressures, and these studies have sought to develop means to re-establish these degraded areas. However, many other vegetation assemblages and areas are subject to natural flooding, such as the Pantanal of Mato Grosso, mangrove forests, and *igapó* forests (seasonally inundated floodplain forests) in Amazonia. Flooding is also occasioned by environmental changes caused by construction of hydroelectric plants, highways that alter the natural drainage, *etc.*

When the soil becomes water-saturated, the rapid decrease in the amount of oxygen available in the soil affects not only the respiratory process of roots and microorganisms, but also the physical and chemical edaphic characteristics. In acid soils such as those predominating in Brazil, waterlogging leads to a significant increase in concentrations of the soluble forms (absorbable by the root system) of ions such as Fe^{2+} and Mn^{2+} . Inevitably, soil pH and redox potential are also altered. In hypoxic and/or anoxic conditions, substitution of aerobic by anaerobic microorganisms may lead to accumulation of gases (CO_2 , NH_3 , H_2S , *etc.*), alcohols (ethanol, butanol, propanol), hydrocarbons (ethylene, butane, propane, methane), phenolic compounds (cumaric acid, ferulic acid), and volatile fatty acids (acetic, butyric, formic) at potentially toxic levels (Ponnamperuma, 1984).

The frequency and duration of soil saturation, whether caused by fluctuations of the water table or by overflow from surface bodies of water, define particular abiotic characteristics at the edaphic as well as at the microclimate levels. These abiotic characteristics significantly affect biotic processes, such as the decomposition rate (Rodrigues, 1989) and the germination and/or recruitment of individuals (Lobo & Joly, 1995; 1996), in such a manner that they end up defining the spatial structure of species along a gradient perpendicular to the river, as well as the composition and structure of the vegetation (Joly, 1994a).

Crawford & Brändle (1996) presented a diagram summarizing the range of adaptations contributing to flood tolerance observed in higher plants. These adaptations can be divided, practically speaking, along two lines. One line represents the strategy of avoiding oxygen deficit through morphological adaptations (aerenchyma), and/or by diffusion of oxygen from the aerial part of the plant to the roots, permitting their aeration. The other line represents adaptive strategies to oxygen deficit, whether through reduction of metabolic rates, removal of toxic products, or changes in metabolism.

Oxygen deficiency at the level of the rhizosphere acts, although slowly, to diminish the permeability of roots to water, reducing its absorption (Slatyer, 1967 *apud* Kozłowski & Pallardy, 1984). Nevertheless, many plants maintain leaf turgor when flooded, which apparently does not lead to reduced water absorption. Regher *et al.* (1975 *apud* Kozłowski & Pallardy, 1984) suggested that in this situation, increased resistance of roots, diminishing water absorption, is accompanied by simultaneous stomate closure, maintaining leaf turgidity.

Exchange of ions between the soil solution and the roots is also altered, whether because of changes in the electrical charges of colloids, or changes in ion concentrations or their charges. Flood-sensitive and flood-resistant plants respond differently to such changes (Kozłowski & Pallardy, 1984; Ponnampuruma, 1984). Transfer of ions from the roots to the aerial parts of the plant may still occur passively through mass flow by means of the transpiration current, although unselectively (Trought & Drew, 1980).

The capacity of the root system to continue performing activities essential to the survival of the individual, such as absorption of water and nutrients and production of plant hormones, depends essentially upon maintaining a minimal pool of phosphated nucleotides (Joly & Brändle, 1995) and of an energy charge (proportion between the concentrations of AMP, ADP, and ATP with a maximum value of 1) greater than 0.5. Under normal conditions the root systems have O_2 available to maintain an aerobic respiratory system, which is highly efficient from the point of view of production of ATP from carbohydrates and permits the cells to maintain an energy charge around 0.8/0.9.

In the absence of O_2 the root system begins to break down carbohydrate molecules anaerobically, which results in low energy production per mole of glucose. To compensate for this low energy yield, the fermentation pathway is accelerated breaking down more moles of glucose per unit time, particularly in anoxia-intolerant species or species tolerant only of short-term flooding such as rice (Crawford & Brändle, 1996). In this case there is a significant increase in the activity of different enzymes, mainly alcohol dehydrogenase (ADH) which is responsible for the last stage of the alcohol fermentation cycle, conversion of acetaldehyde into ethanol. This strategy depends on an unlimited supply of carbohydrates, generally transported from the aerial part to the root system. Acceleration of glycolysis can generate a considerable quantity of ethanol and lactate, the concentrations of which may attain toxic levels within the cells. Ethanol, being an organic solvent, can destructure the plasma membrane, solubilizing the lipid components

(Crawford, 1978). Lactate (lactic acid) alters cytoplasm pH, inhibiting important enzyme complexes and leading to cell death (Roberts *et al.*, 1985).

Considering these aspects, Crawford (1978) hypothesized that flood-tolerant plants would avoid the alcohol and lactic fermentation pathways, and would activate an alternative route leading to malate production and accumulation. Malate is a weak acid which, upon accumulating in the vacuoles, does not alter cytoplasmic pH and is a four-carbon compound, part of the Krebs cycle. Consequently, when the root system again has access to O_2 , malate can be oxidized, generating ATP. Critics of this proposal (Smith & Ap Rees, 1979; Davies, 1980) emphasized mainly the fact that the alternative pathway proposed by Crawford (1978) would theoretically not generate ATP.

However, if we consider the possibility that ATP production is allied to oxygen diffusion from the aerial part to the root system, the route proposed by Crawford (1978), in addition to helping maintain the cell redox potential, would play the fundamental role of detouring phosphoenol pyruvate from the fermentation pathway, avoiding high production of ethanol and/or lactate (Joly, 1994b). This reinterpretation of the role of malate in the root system of flood-tolerant plants was recently proposed by Joly (1994b).

In spite of the problems previously described, some species such as rice show a strong acceleration of the alcohol fermentation pathway with extremely high alcohol production. The ethanol, however, is diffused through the surrounding aqueous medium and does not accumulate in the root cells (Bertani *et al.*, 1980). The mechanisms permitting this diffusion are not yet well understood. Other tolerant species avoid production of ethanol, accumulate malate, and reduce their root system metabolism, adjusting it to the amount of O_2 diffused from the aerial part (Joly & Crawford, 1982).

Water saturation of soil can induce development of some morphological and anatomical changes, such as hypertrophy of lenticels, development of adventitious roots, and development of aerenchyma at the base of the stem and in the rhizomes (see also the review by Pimenta *et al.*, in this volume). These modifications are generally associated with increased capacity for O_2 diffusion from the aerial part to the root system. However, it is worth remembering that these responses do not always have adaptive value, since they may be a response to significant changes in the process of synthesis and/or transport of hormones such as auxin and ethylene, without leading to increased O_2 diffusion to the root system. Therefore, simply establishing that these changes occur cannot be used as a criterion to classify species as tolerant or intolerant of soil waterlogging.

Hypertrophy of lenticels is induced by ethylene (Bradford & Yang, 1981; Kawase, 1981) and generally occurs at the base of the stem. However, similar structures may also appear in the root system, especially at the bases of secondary roots. Hypertrophic lenticels are generally associated with large intercellular spaces in neighboring cortical layers (Hook & Scholtens, 1978), that are observed in the stem and roots. These function as entry points for air (Lobo & Joly, 1995; Joly, 1996) that passively

diffuses through these spaces and reaches the root tips, the growth zone, where metabolic demand is high. Chirkova & Gutmann (1972) and Hook & Scholtens (1978) showed that hypertrophic lenticels can also act as exit points for volatile compounds such as ethylene, ethanol, and acetaldehyde produced by flooded roots and transported to the aerial part. However, Crawford & Finegan (1989) pointed out that these gaseous ports of exit only remove a minor part of the total amount of ethanol.

The role of ethylene in inducing the formation of aerenchyma has been proven by the absence of this response in flooded plants treated with inhibitors of this phytohormone (Drew *et al.*, 1981; Kawase, 1981; Konings & Lambers, 1991). Aerenchyma may originate from cell separation (schizogeny) or from breakdown of cortical cells (lysogeny), forming continuous gas-filled lacunae (Jackson & Drew, 1984). The participation of ethylene in forming lysogenic aerenchyma in corn plants submitted to oxygen deficits is clearly elucidated, since the programmed death of certain cells is preceded by degradation of the cell wall, which is associated with increased concentration of cellulases. Schizogenic aerenchyma formation as well as the importance of other phytohormones remain neglected as subjects for experimentation (Armstrong *et al.*, 1994).

Flooded plants frequently develop new surface roots (Hook, 1984; Lobo & Joly, 1995) and/or adventitious roots (Wample & Reid, 1979; Sena Gomes & Koslowski, 1980; Joly & Crawford, 1982; Newsome *et al.*, 1982; Lieberg, 1990; Marques, 1990; Lobo & Joly, 1995). These roots generally have few branches and are more porous and straighter than the older ones. High porosity, besides facilitating diffusion of gases, also shows that in these roots a small proportion of their tissues is metabolically active and therefore has a high O₂ demand in relation to the surface area available for absorbing water and nutrients. In this manner, many root functions can be maintained and growth is possible (Sena Gomes & Koslowski, 1980; Drew *et al.*, 1985; Konings & Lambers, 1991).

Part of the O₂ diffused from the aerial part to the root system is not utilized for respiratory metabolism, but is diffused through the root surface, creating an oxidant rhizosphere which permits restoration of ion absorption and growth (Engelaar *et al.*, 1993). This is one of the mechanisms developed to avoid excessive absorption of iron and manganese ions which, when oxidized, become insoluble and are deposited on the root surface. Considering that in gallery forests and marshes in southeastern Brazil the depth of the water above the soil is generally a few centimeters, these surface and/or adventitious roots are developed in an environment relatively aerated in relation to the soil where the original root system is located. The original root system invariably drastically reduces metabolic activity, halts growth, and functions almost exclusively to fix the individual in the soil. This function is vitally important, for example, in the large river floods. These floods are usually of short duration (several days), when the water can deepen to more than a meter and be considerably destructive to root systems.

Evidently, mechanisms of O₂ diffusion to the root system presuppose that the aerial part is emergent. There are practically no studies of neotropical shrubby species, or of young individuals of tree species, that remain submerged for months, as is the case for the species of the Amazonian *igapó* and *várzea* forests. One of the few species studied is the palm *Astrocaryum jauari* (Schlüter *et al.*, 1993). Under conditions of complete submersion, besides reduced exchange of gases there are also changes in light conditions that doubtless affect photosynthesis. Thus, plants that, when submerged, are capable of photosynthesis at low CO₂ levels and reducing respiration rates, have a great advantage (Clevering *et al.*, 1995 *apud* Blom & Voesenek 1996).

Other physiological changes can be observed in roots of flooded plants. Anaerobiosis induces an increase in the endogenous levels of ACC, the precursors of ethylene. ACC is transported via the xylem to the aerial part of the plant where it is converted to ethylene (Bradford & Yang, 1981) and induces a series of responses. Auxin levels are also elevated, whether by interference in its production in the roots, or in its basipetal transport. As roots are the organs that synthesize gibberellins and cytokinins, these phytohormones also have their endogenous levels reduced (reviewed by Reid & Bradford, 1984). Although the increase in ABA levels in stressful conditions is a very common response in plants, the origin of this increase is still much debated (Jackson, 1993).

Certain changes are also observed in the development of the aerial part of plants whose roots are flooded. Closing of stomata and reduction in the photosynthesis rate are effects observed in trees as a result of O₂ deficiency in the soil (Newsome *et al.*, 1982; Tang & Kozlowski, 1982; Pezeshki, 1993). However, there are many variations in this response pattern, whether related to the greater or lesser degree of tolerance of the species (Sena Gomes & Kozlowski, 1988), or to leaf age and the time when flooding begins (Bradford & Hsiao, 1982; Newsome *et al.*, 1982).

Species tolerant to waterlogging can resume photosynthesis more rapidly than sensitive species, during flooding as well as afterwards (Pezeshki, 1993). Evidently, this characteristic is fundamentally important for carbohydrate production and transport, in order to meet the new demand imposed by metabolic changes occurring in the root system.

In the case of intolerant species, soil saturation inhibits growth and induces premature senescence, chlorosis, leaf abscission (Tang & Kozlowski, 1982), and degeneration of the root system (Kozlowski, 1984). However, the biochemical processes that affect the capacity for photosynthesis as a result of root stress are little understood (Pezeshki, 1994). In any event, lack of oxygen in plant tissues can lead to death in several ways, whether by promoting metabolic disfunctions that cause changes in membrane functions, possibly leading to cytoplasmic acidosis; or by intoxication through absorption of Mn²⁺ and Fe²⁺ ions or as a consequence of damage from re-aeration of postanoxic tissues, which can lead to formation of highly toxic compounds (Crawford & Brändle, 1996).

Not only roots and rhizomes are subject to soil waterlogging and its consequences. Flooding influences seed dispersal, the characteristics of the seed bank, germination, emergence, seedling establishment and survival, as well as growth and reproduction (Blom *et al.*, 1990 *apud* Blom & Voesebeck, 1996). Thus it is necessary to study the life cycle phases of plants exposed to possible damage from lack of oxygen (Crawford & Brändle, 1996; see also the review by Scarano, in this volume).

Seeds can be dispersed by water or fall onto flooded soil. After hydration, seeds naturally pass through an anaerobic process because of the impermeability of the seed coat to O₂, and because of high metabolic activity (Crawford, 1992; Vazquez-Yanes & Orozco-Segovia, 1993). However, O₂ is necessary for generating the energy needed for germination in the overwhelming majority of species.

Extremely well-studied exceptions are the germination and growth under anaerobic conditions of seeds of rice (*Oryza sativa*) and of *Echinochloa phyllopogon*, a weedy grass that frequently grows in association with rice (Pradet & Bomsel, 1978; Davies, 1980; Rumpho & Kennedy, 1983; Kennedy *et al.*, 1991). The tolerance of seeds and seedlings of *E. phyllopogon* (a synonym of *E. crusgalli* var. *oryzicola*) to anaerobiosis is a result of its capacity to liberate a large part of the ethanol produced to the external medium, and to metabolize part of the ethanol intracellularly, being capable of tolerating high amounts of this metabolite (Rumpho & Kennedy, 1983). Other metabolic activities such as the oxidative pentose-phosphate pathway and lipid synthesis are extremely important in conferring this tolerance to anoxia (Kennedy *et al.*, 1991) and in maintenance of an energy charge of approximately 0.8, even in the absence of oxygen (Rumpho & Kennedy, 1983).

In regard to tropical species, *Chorisia speciosa* (Joly & Crawford, 1983) and *Erythrina cafra* (Small *et al.*, 1989) have seeds capable of producing rootlets under anaerobic conditions, although only after cell expansion following hydration and without further development of the seedlings.

Germination and subsequent seedling growth in hypoxic conditions (waterlogging) are responses observed only for seeds of *Inga affinis* (Lieberg & Joly, 1993), a common species of gallery forests, and for seeds of *Sesbania virgata* (Okamoto, 1995). Seeds of *Talauma ovata*, a typical species of marshy scrublands, do not germinate while immersed or in water-saturated soils (Lobo & Joly, 1996). Young individuals, however, tolerate long periods of inundation (Lobo & Joly, 1995). Perpetuation of the species is guaranteed by seed dispersal, mainly by birds, during the dry season when as a result of the topographic heterogeneity of the marshy scrublands, there are well-drained micro-sites favorable to germination.

Seeds of other species such as *Parkia pendula* and *P. discolor*, legumes inhabiting Amazonian *terra-firme* (unflooded) and *igapó* (flooded) forests respectively, have a hard seed coat and tolerate up to seven months of submersion, germinating when they are scarified and transferred to aerated conditions (Scarano & Crawford, 1992).

The wide array of morphological, anatomical, physiological, and metabolic responses observed in herbaceous and shrubby plants and trees native to environments that are subject to seasonal or permanent soil waterlogging makes it difficult to establish criteria for defining tolerance to such stress. In the present state of understanding regarding these responses in neotropical species, some homogenization of criteria is necessary. We consider as "tolerant" only those species that succeed in maintaining or increasing the dry weight of the aerial part, when submitted to stress for periods comparable to those to which they would be subject in their native habitats. This characteristic is essential to ensure a competitive advantage permitting the individuals of such a species to successfully establish themselves in areas subject to flooding.

Considering the period usually used in experiments on tolerance to waterlogging (rarely more than 60 days), survival of the individuals studied may occur at the expense of accumulated reserves, and/or at the expense of photosynthates necessary to maintain essential metabolic activities. Such a species would have difficulty in successfully establishing itself, attaining the reproductive phase, and disseminating propagules in areas naturally subject to flooding. It is appropriate to emphasize that under natural conditions, besides inter- and intraspecific competition, the duration, intensity, and recurrence of stress from soil saturation are unpredictable.

Aspects of flood tolerance and adaptive strategies of some Neotropical tree species

Tolerant species

***Sebastiania klotzchiana* M. Arg. - Euphorbiaceae (Joly & Crawford, 1982; Joly, 1991).** A species of tree common in gallery forests and in flood-prone locations such as sedimentary dikes along rivers. Growth of the aerial part is not inhibited by soil saturation, no morphological modifications were observed, and oxygen diffusion from the aerial part to the root system was observed in four-month-old plants flooded for 30 days. During this period, acceleration of the fermentation pathway was observed, with a ninefold increase in ADH activity in the roots. The main end product of anaerobic metabolism was ethanol. In spite of a significant reduction in respiratory metabolism after 30 days of flooding, the concentration of ethanol found in the root system corresponds to less than 5% of the total estimated production. This suggests that the species must have mechanisms to diffuse ethanol to the aqueous medium surrounding the roots. The occurrence of this species in areas where the floodwaters are always moving would permit constant removal of the ethanol, avoiding accumulation to toxic levels. The presence of numerous starch grains in the roots of this species (Rosana M. Kolb, personal communication) suggests that there is no limitation in this substrate to maintain high levels of anaerobic metabolism.

***Inga affinis* DC. - Mimosaceae (Lieberg, 1990; Lieberg & Joly, 1993).** A tree species also typical of sedimentary dikes. Flooding does not inhibit plant growth,

which tends to be slower than growth of control plants only after 80 days of inundation. The original root system dies and is replaced by new, white, thicker roots. Hypertrophy of lenticels occurs after 15 days of inundation. Adventitious roots, more porous than the original ones, are formed after 30 days. The seeds are not photoblastic and germinate even when submerged, forming seedlings capable of developing underwater.

***Astrocaryum jauari* Mart. - Arecaceae (Schlüter *et al.*, 1993).** Young plants of *Astrocaryum jauari* show anatomical and physiological adaptations to conditions of low oxygen availability. Even after 300 days of inundation, the plants do not lose their leaves and the roots are still viable. In *igapó* forests the chlorophyll content of leaves of plants totally submerged beneath 1.2 meters of black water is only slightly reduced. However, if submersion occurs in the clear water of a *várzea* forest, there is significant chlorophyll loss. The consequence of these differences can be noted, for example, in the rate of oxygen production by photosynthesis. Beneath black water the rate of photosynthesis is 30%, and under clear water it hardly reaches 10% of that observed in emergent plants. The respiratory metabolism of roots decreases significantly during the high water period, and ethanol is the main product of anaerobic metabolism. In plants with the aerial part emergent, diffusion of gases from the aerial part to the root system is assured by the presence of a well-developed aerenchyma. The presence of a solid sclerenchyma impedes the collapse of the root aerenchyma, in spite of a significant increase in water pressure.

***Sesbania virgata* (Cav.) Pers. - Fabaceae (Davanso, 1994; Okamoto, 1995).** Shrubby species frequently found along the banks of rivers, reservoirs, *etc.* Experimental flooding for 30 days does not inhibit growth, which is even faster than the growth of control plants. After inundation the stem and plants show longitudinal fissures, exposing spongy cortical tissue. Anatomical changes are also observed in the parenchyma tissues of the stem-culm region and in the roots. Hypertrophic lenticels are not observed, but adventitious roots are well developed. The seeds of *S. virgata* are photoblastically neutral and scarification of the testa, which is done by fish (Orsi *et al.*, 1994) accelerates the germination process. Scarified seeds germinate while inundated, giving rise to seedlings that develop while submerged. Anoxia, imposed artificially in special jars, inhibits germination but does not kill the seeds, which germinate promptly when transferred to aerobic conditions. Ethanol is the chief metabolite of anaerobic respiration, and is easily eliminated in an aqueous medium.

***Hymenaea courbaril* var. *stilbocarpa* Lee et Lang. - Caesalpinaceae (Joly & Crawford, 1982; Joly, 1991).** Tree species found in gallery forests, in the depressions behind dikes along rivers, and in moist areas of semideciduous forests. The growth of flooded plants is significant, although slower than if the plants are maintained in well-drained conditions. Morphological and anatomical modifications were only observed in the new, more porous roots formed upon flooding. After 30 days of inundation, ADH activity was less than that detected in control plants. Endogenous levels of the metabolite

malate increased the most, however only up to day 8 of treatment. Even in the absence of hypertrophic lenticels, diffusion of O_2 to the root system was observed. The seeds do not germinate when scarified and kept submerged.

***Genipa americana* L. - Rubiaceae (Joly, 1982).** Tree species typical of depressions behind sedimentary dikes. Flooding does not inhibit growth of the aerial part, and new, more porous roots are observed in the flooded plants. The seedlings, as opposed to juvenile individuals, do not show morphological or anatomical modifications at the base of the stem. With flooding there is a threefold increase in ADH activity, and ethanol is the main product of anaerobic metabolism. Root respiration is unaffected, and O_2 diffusion from the aerial part is not observed.

***Talauma ovata* St Hil. - Magnoliaceae (Lobo & Joly, 1995; 1996).** Tree species, typical of marshy scrublands and in gallery forest sites prone to periodic, long-term flooding. Flooding does not inhibit growth, but growth is slower than in control plants. After 6 days of inundation, hypertrophy of lenticels occurs, and new surface roots and additional adventitious roots, both more porous, appear after 30 days. With hypoxia, ADH activity in the root system shows a tenfold increase by day 10, after which ADH activity remains 3 times higher than in the control plants. An increase in ethanol levels is also observed in the roots of flooded plants, however on a smaller scale. Diffusion of O_2 to the root system is observed, the lenticels functioning as entry points for air. Seeds are dispersed during the dry season and are incapable of germinating when submerged, but remain viable for about 15 days under these conditions.

***Calophyllum brasiliense* Camb. - Clusiaceae (Marques, 1994).** Tree species, quite common in locations prone to long-term flooding in gallery forests, marshy scrublands, and particularly characteristic of the Atlantic forest at sites where the groundwater surfaces. Flooding does not affect plant growth, which was slow under experimental conditions. Hypertrophic lenticels form at the base of the stem after 10 days of inundation, and new roots form after flooding. Seeds do not germinate when submerged, but remain viable for a lengthy period, germinating upon transference to aerated conditions.

***Chorisia speciosa* St. Hil. - Bombacaceae (Joly & Crawford, 1982; Joly & Crawford, 1983; Joly, 1991).** Tree species typical of semideciduous and deciduous forests. Frequently occurs in areas subject to sporadic flooding during exceptional floods, in the transition zone to gallery forest. Plant growth is not inhibited by flooding, but is slower than in control plants. After 10 days of flooding, hypertrophy of lenticels occurs and there is induction of aerenchyma at the base of the stem. Simultaneously, new, more porous superficial and adventitious roots appear. After 1 month of inundation, the plants show a 2.5-fold increase in ADH activity, and greater O_2 consumption by the roots. Diffusion of O_2 into the roots is also detected, the lenticels serving as entry points for air. Seeds of *C. speciosa* placed to germinate in anoxic conditions show protrusion of the seed radicle with a rapidity and percentage of final germination similar to seeds maintained in normal oxygenated conditions. However, the subsequent development of

seedlings is inhibited under anoxic conditions, suggesting that the protrusion of the seed root occurs mainly as a result of cell expansion.

***Copaifera langsdorffi* Desf. - Caesalpinaceae (Joly, 1982; Machado, 1990).**

Tree species, widely distributed in semideciduous forests, cerrado/cerradão (savanna and savanna with significant tree canopy), and gallery forests. Prolonged flooding inhibits growth of the plants, which, however, survive up to 8 months in these conditions. No morphological changes occur at the base of the stem or in the roots, which however are anatomically different, being more porous. A 2.5-fold increase in ADH activity is observed. Endogenous levels of ethanol, malate, and lactate are all elevated. The seeds, which require scarification in order to germinate, are dispersed at the end of the dry season, are viable for a long period, and do not germinate when submerged.

***Hedychium coronarium* J. G. Koenig - Zingiberaceae (Joly & Brändle,**

1995). Although not a Neotropical species, *H. coronarium* was studied and is included here because of its wide distribution in Brazil. It is a rhizomatose monocotyledon, originating in India, which was introduced to Brazil about 300 years ago and has become an important invader of riverbanks, swamps, and areas subject to flooding. The *lírio-do-brejo* or butterfly lily grows aggressively and its aerial part may attain a height of 2 m. The plants may impede the natural regeneration of gallery forests because of outcompeting the seedlings of other species. When the rhizomes (without the aerial part) are maintained under hypoxic conditions for up to 8 days, they continue to grow normally; after 16 days however their development is slower. Anoxic situations affect growth after only 8 days, and lead to greater production of ethanol and lactate compared to hypoxic conditions. Evaluation of the energy charge (relationship between quantities of nucleotides) showed that there is a perceptible reduction in energy charge soon after hypoxia or anoxia begins, falling from 0.8 to 0.5. There was a significant reduction in total available nucleotides mainly in rhizomes maintained under anoxic conditions. This reduction is possibly associated with lactate accumulation and the subsequent decrease in cell pH. Rhizomes maintained under anoxic conditions die between 8 and 16 days of treatment, while those maintained in hypoxic conditions for up to 16 days still show full recuperative capacity when returned to a normal atmosphere. Therefore this is a species whose rhizome is tolerant of hypoxic conditions and intolerant of long-term anoxia which, under natural conditions, depends on the diffusion of oxygen from the always emergent aerial part. The presence of a well-developed aerenchyma in the aerial part as well as in the rhizome itself reinforces this hypothesis. The results obtained permit the development of a control method for this aggressive invader. Cutting the aerial part of the stands along riverbanks at the beginning of flood season impedes oxygen diffusion from the aerial part to the rhizome, which is then submerged in conditions of extremely low oxygen availability. A period of 15 to 20 days in this conditions will lead to death of the rhizomes, avoiding their propagation and creating conditions for establishment of seedlings of native plants typical of these periodically inundated areas.

Intolerant species

***Cedrela fissilis* Vell. - Meliaceae (Lobo, 1990; Marques, 1990; Marques *et al.*, 1992).** Tree species present in semideciduous forests, or in areas with well-drained soils not influenced by rivers. Flooding for 60 days inhibits growth of the plants and induces chlorosis and leaf abscission. The stem base of inundated plants appears more porous, and hypertrophic lenticels and adventitious roots are observed after 15 and 25 days respectively. The adventitious roots are extremely important to flooded plants, since experimental removal leads to reduced growth when compared to flooded plants retaining these structures. Initially there is a decrease in root respiration (10 days) which then returns to normal levels (60 days). The seeds do not germinate when submerged, but remain viable for about 10 days, when they germinate if returned to aerated conditions.

***Schyzolobium parayha* (Vell.) Blake - Caesalpinaceae (Joly & Crawford, 1982; Joly, 1991).** Tree species, common in semideciduous forests and infrequent in gallery forests, occurring in well-drained areas. Flooding inhibits growth of the plants and induces the appearance of longitudinal fissures, exposing spongy cortex tissue. In spite of the presence of this spongy tissue, it was not possible to observe oxygen diffusion from the aerial part to the root system of plants submitted to flooding for 1 month. Upon inundation there was a twofold increase in ADH activity. The ethanol level increased as of day 2 and was progressive until day 8, after which it stabilized. Malate and lactate levels did not change significantly during flooding.

***Enterolobium contortisiliquum* (Vell.) Morong - Mimosaceae (Joly, 1982).**

Tree species commonly occurring in cerradão, semideciduous forests, and gallery forests. Flooding inhibits growth of the plants and induces hypertrophy of lenticels. There is oxygen diffusion from the aerial part to the root system. Apparently, the hypertrophic lenticels are not the only point of entry for oxygen, because if these structures are removed, oxygen diffusion continues, although at a significantly lower level. Saturation of the soil by water induces up to a fourfold increase in ADH activity, although levels of ethanol and lactate do not change significantly during inundation. On the other hand, the level of malate, which is unusually high in control plants (10 mmol.g⁻¹ fresh weight), reaches 12 mmol.g⁻¹ fresh weight on the second day and afterwards decreases gradually to about 2 mmol.g⁻¹ fresh weight. No logical interpretation was found for the responses observed in this species. Anoxia inhibits germination of scarified seeds of *E. contortisiliquum*, so that after 48 hours of treatment they are incapable of germination even if transferred to a normal atmosphere. In the course of germination, ethanol is the main metabolite accumulated, in seeds maintained in air as well as in seeds under anoxic conditions.

***Peltophorum dubium* (Spreng) Taub. - Caesalpinaceae (Joly, 1982).**

Tree species, common in semideciduous forests, infrequent in gallery forests, occurring in well-drained areas. Flooding inhibits growth of the plants and induces hypertrophy of lenticels and formation of some new, more porous roots. Upon inundation there is a twofold increase in ADH activity. The level of ethanol begins to increase after day 2 and

this increase is progressive until day 8, after which it stabilizes. Malate levels also increase after day 2, peak on day 4, and then return to the base level. Scarified seeds do not germinate under anoxic conditions, but survive up to 48 hours without oxygen. Ethanol is the main accumulated metabolite, in seeds maintained in air as well as in those kept in anoxic conditions.

***Hevea brasiliensis* Muell. Arg. - Euphorbiaceae (Sena Gomes & Kozłowski, 1988).** Flooding for 12 weeks reduces the relative growth rate of 45-day-old seedlings of three cultivars of this species, and also inhibits leaf formation. At the end of the second week, hypertrophy of lenticels in the submerged part of the stem and epinasty of the younger leaves were observed, as well as formation of white, poorly branched, succulent adventitious roots; fissures at the base of the stem; and maintenance of stomate opening. As a consequence of flooding there was also a reduction in chlorophyll a content, and ethylene was liberated by the leaves and roots. The authors suggest that the species tolerates only short periods of inundation.

Final considerations

The permanent or temporary presence of water in the soil determines floristic and physiognomic differences between *igapó* forests, várzea forests, marshy scrublands, riparian forests, and semideciduous mesophilic forests (Leitão Filho, 1982; Joly, 1986; Mantovani, 1989; Rodrigues, 1989). Characteristics such as environmental heterogeneity resulting from macro- and micro-topography, the low floristic diversity of the tree layer, and the perennially leafy character because of long-lived or rapidly replaced/repositioned leaves, of the areas subject to water saturation, contrast with the characteristics of the adjacent mesophilic forests (Leitão Filho, 1982), demonstrating the determining role of soil saturation. The floristic diversity of the tree layer of these formations subject to soil saturation is inversely proportional to the intensity, duration, and recurrence of the stress. In the depressions behind the sedimentary dikes of riparian forests, the soil remains saturated for a long period of time with stagnant water (movement occurs only vertically, depending on fluctuations in the water table). This is because the saturation results from a rise in the water table and/or from retention of river floodwaters. On the dikes, inundation lasts only a few hours or at most for several days, and the water is continually renewed. In marshy scrublands, the hydromorphic soils remain water-saturated during most of the year, and waterlogging becomes less evident only in winter. At this season it is possible that the rate of photosynthesis and consequently the growth rate is lower than in summer, as a result of lower temperatures and reduced levels of photosynthetically active radiation (PAR).

During the course of evolution, these peculiarities acted differently in selection of adaptive strategies of the species typical of each environment. A detailed review of floristic and phytosociological studies, emphasizing the areas effectively subject to soil saturation, provides evidence that the exclusively or preferentially hygrophilic species, besides being few in number, generally occur from the Tropic of Capricorn to the Tropic of Cancer and always in areas subject to flooding. This wide geographical distribution

contrasts with their marked habitat specificity. Species typical of dikes (such as *Inga affinis* and *Sebastiania klotzchiana*) rarely occur in the adjacent depressions or in marshy scrublands. Species typical of depressions (such as *Hymenaea courbaril* var. *stilbocarpa* and *Genipa americana*) rarely occur in marshy scrublands or on the dikes. Species typical of marshy scrublands (such as *Talauma ovata* and *Calophyllum brasiliensis*) rarely occur in the other two environments.

This marked specificity may be a consequence of the competitive disadvantage which a given adaptive strategy may signify in environments different from that which it was selected for in the course of evolution. The competitive disadvantages may also explain the absence of these species from well-drained environments of adjacent forest formations, in spite of the fact that the majority of these species do quite well when grown under in well-drained conditions. These conjectures pay respect, obviously, not only to the mechanisms developed by the root system to tolerate the period of soil saturation, but also to the longevity and photosynthetic efficiency of the leaves, and to the efficiency of the root system in absorbing water and nutrients.

It is appropriate to point out the probability that specific physical and chemical characteristics of the soils, and the changes which these undergo during the period of saturation, also played an important role in selecting for the species that today are typical of each environment. The changes in chemical characteristics of the thick clay layer covering the surface of the hydromorphic soils of marshy scrublands are, without doubt, completely different from those that occur in the mostly sandy soils of the alluvial plain occupied by the gallery forests.

Therefore the necessity becomes evident for studies of the adaptive strategies of the species that naturally occupy these seasonally or permanently inundated habitats. However, it should be borne in mind that during the evolutionary process, morphological, anatomical, physiological, and biochemical processes evolved concomitantly and quite possibly complementarily. Thus their understanding requires studies treating these aspects in conjunction, complementing when possible studies of demography and population dynamics.

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