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Variation in Tolerance and Metabolic Responses to Flooding in some Tropical Trees

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ABSTRACT

The effect of flooding on aerobic and anaerobic respiration as well as on the internal levels of ethanol, lactic, succinic and malic acids were compared in three flood-tolerant and two non-flood-tolerant species. In the non-flood-tolerant species *Kielmeyera coriacea* and *Pseudobombax marginatum*, which come from the 'cerrado' vegetation, there was a uniformity of response with ethanol being the only one of the above products to accumulate substantially during flooding. In the flood-tolerant species, *Sebastiania klotzchyana*, *Hymenaea courbaril* var. *stilbocarpa* and *Chorisia speciosa*, flooding induced a variety of responses which indicate that the tolerant species have evolved differing strategies to overcome flooding stress.

INTRODUCTION

The flood-plain and river gallery forests of the tropics are habitats in which many tree species have to endure regular and sometimes prolonged periods of flooding (Ratter, Richards, Argent, and Gifford, 1973). However, despite the richness and extent of such riverine habitats in the tropics, little is known of the mechanisms which enable the trees to maintain healthy root systems in soils that can be expected to be highly anaerobic when flooded.

The only tropical tree which has received extensive physiological investigation in relation to its flooding tolerance is *Nyssa sylvatica* (Hook, Brown, and Kormanik, 1971; Keeley, 1978, 1979; Keeley and Franz, 1979). Hook *et al.* (1971) concluded that the flood tolerance of this species depends on the capacity to accelerate anaerobic respiration and to oxidize the rhizosphere. These conclusions were corroborated by Keeley (1978, 1979) and Keeley and Franz (1979), although this latter paper regards the new root system of *Nyssa sylvatica* with high anaerobic respiration rates observed by Hook *et al.* (1971) as a short-term adaptation. The long-term adaptation being the subsequent replacement of these roots and an increase in the oxygen transport to the root system (Keeley and Franz, 1979). Apart from this species, studies of tropical trees have been restricted to mangroves (Brown, Outred, and Hill, 1969), and to general floristic surveys (Klein, 1963; Ratter *et al.*, 1973; Gibbs and Leitão Filho, 1978; Furness and Breen, 1980; Harms, Schreuder, Hook, Brown, and Shropshire, 1980).

To extend the knowledge of flooding tolerance in tropical vegetation this present study examines the responses of five Brazilian tree species to flooding. Two of the species, *Kielmeyera coriacea* (Spr) Mart. (Guttiferae) and *Pseudobombax marginatum* (St. Hill.)

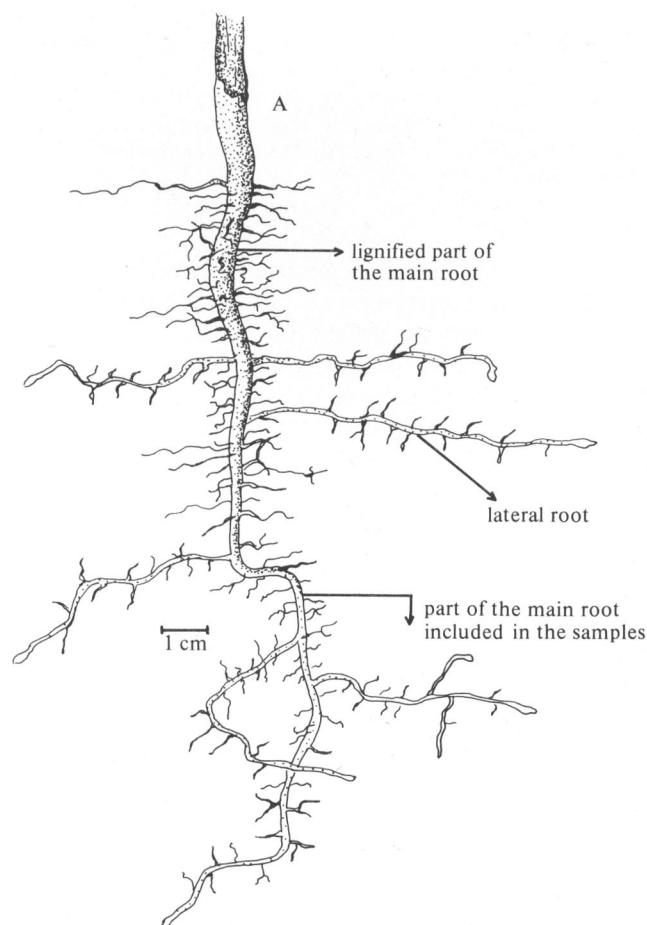
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Robyn (Bombacaceae) are typical 'cerrado' species (Heringer, Barroso, Rizzo, and Rizzini, 1977); 'cerrado' is a savannah-like vegetation occurring in well-drained soils which are never waterlogged (Eiten, 1972). *Sebastiana klotzchyana* M. Arg. (Euphorbiaceae) is a tropical gallery forest species, restricted to flood prone areas where it is often co-dominant (Klein, 1963; Gibbs and Leitão Filho, 1978). *Hymenaea courbaril* L. var. *stilbocarpa* Lee et Lang (Leguminosae-Caesalpinioideae) does occur in gallery forests (Ratter *et al.*, 1973; Gibbs and Leitão Filho, 1978), but is not restricted to this community being also found in dry forests. *Chorisia speciosa* St. Hill. (Bombacaceae) is a typical dry forest species (Rizzini, 1979) being rare in areas that are seasonally flooded.

MATERIALS AND METHODS

The seeds of *Sebastiana klotzchyana* and *Hymenaea courbaril* var. *stilbocarpa* were collected in the gallery forest of the Experimental Station of the Forestry Institute of the State of São Paulo, while seeds of both cerrado species, *Pseudobombax marginatum* and *Kielmeyera coriacea*, were collected in the reserve of the Botanical Institute of São Paulo; both communities are situated in the municipal district of Mogi Guaçu, state of São Paulo, Brazil (22° 18' S, 47° 13' W). The seeds of *Chorisia speciosa* were collected in the same area.

The seeds were sown in washed river sand in 12 cm diameter plastic pots and the emergent seedlings were watered once a week with 1/5 strength Hoagland's solution. Experimental flooding was carried out by transferring pots with 3- to 4-month-old seedlings to plastic basins where they were maintained



with a water level 2–3 cm above the soil surface. The water was changed weekly as in the natural environment the water is never entirely stagnant.

The flooded plants were observed every week, and the following characteristics were scored: initiation of new leaves; development of the apex; morphology of the stem, particularly the submerged area and that just above the water surface.

The accumulated growth during 1 month's flooding was used to classify the species as flood-tolerant or intolerant (Crawford, 1966).

The respiration of the roots was measured in Warburg flasks at $25 \pm 1^\circ\text{C}$ either under air or after gassing with oxygen-free nitrogen (Crawford, 1966). The roots were surface sterilized with 0.02% mercuric chloride, washed in sterile water and placed in flasks containing 2.0 ml of 0.05 M phosphate buffer pH 5.4 plus 1% sucrose (Crawford, 1977). Each sample consisted of segments of the secondary root system and the apex of the primary root of one plant (Fig. 1). The lignified parts of the roots and the 'ligno tuber' (Rizzini and Heringer, 1962) of the cerrado species were not included in the samples (see Fig. 1). Care was taken to try and exclude dead material, particularly for the measurements with flooded roots. After 4 h the roots were harvested in ice cold 6% HClO_4 and extracted for ethanol determination (Bergmeyer, 1974). The flasks were rinsed with ice cold distilled water which was included in the sample together with the incubation medium.

The pattern of accumulation of the glycolytic and related metabolites in the roots was studied in plants flooded for 1, 2, 4, 8, 16 and 32 d. When harvesting, the sand was carefully removed from the roots which were blotted dry, weighed and harvested in ice cold 6% HClO_4 . The samples were extracted for ethanol, malate, lactate and succinate determinations (Bergmeyer, 1974). Obviously during the treatment a considerable amount of metabolites must have been exchanged with the medium and with the aerial part of the plants, just as would be expected in the natural environment. These estimates were not intended to measure the production of metabolites during the treatment, but were carried out to provide comparative data on the different strategies developed by the species studied, i.e. accumulation or not of potentially toxic metabolites.

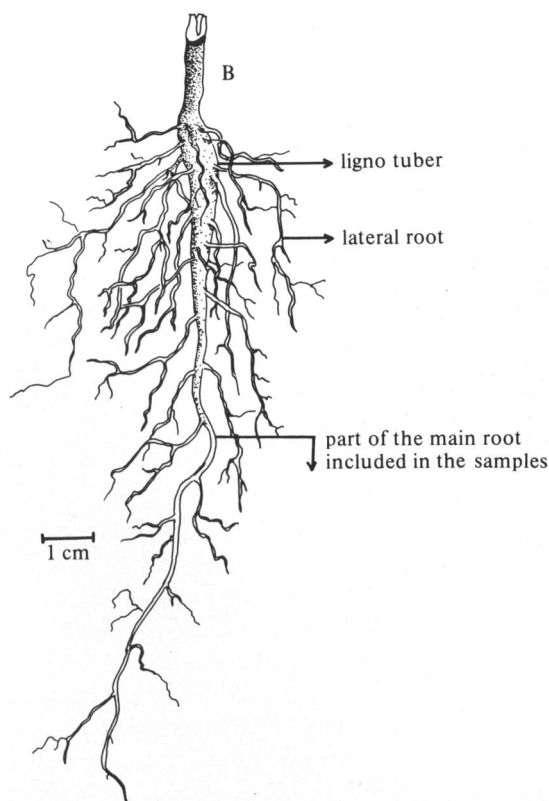


FIG. 1. Root systems of 3-month-old plants of *H. courbaril* var. *stilbocarpa* (A, gallery forest) and *P. marginatum* (B, cerrado).

The significance of the increase in dry weight of the shoots of 3-month-old seedlings subsequently flooded for 1 month ($n = 10$) and in the respiratory metabolism of the roots of these plants ($n = 4$) was tested by a t test. Analyses of variance with the determination of LSD was applied to test the significance of the changes in the levels of the metabolites accumulated during the flooding experiment. The correlation in Fig. 4 was tested by the determination of t with ($n = 2$) degrees of freedom.

RESULTS

(1) Growth responses to flooding

None of the plants died during the flooding treatments, and all were able to resume growth when the stress was removed. In the cerrado species, *P. marginatum* and *K. coriacea*, growth was inhibited by flooding while the three species, *S. klotzchyana*, *H. courbaril* and *C. speciosa*, continued to grow and showed a significant increase in shoot dry weight during the treatment (Table 1).

TABLE 1. Dry weight (g) of shoots of 3-month-old plants (control) and of plants subsequently flooded for 1 month

Community	Species	Control	Flooded	P
Gallery forest	<i>Sebastiania klotzchyana</i>	1.095 ± 0.089	1.778 ± 0.210	<0.05
Gallery forest	<i>Hymenaea courbaril</i> var. <i>stilbocarpa</i>	3.872 ± 0.413	4.769 ± 0.127	<0.05
Dry forest	<i>Chorisia speciosa</i>	1.513 ± 0.176	2.180 ± 0.274	<0.05
Cerrado	<i>Kielmeyera coriacea</i>	0.334 ± 0.024	0.367 ± 0.018	NS
Cerrado	<i>Pseudobombax marginatum</i>	0.796 ± 0.101	0.796 ± 0.101	NS

The development of the three forest species, which continued to grow while flooded, showed no morphological abnormalities. The apex and leaves grew as in the control plants and new leaves appeared as in the controls. In *C. speciosa*, a dry forest species, after 10 d of flooding, hypertrophic lenticels were observed in the submerged part of the shoots just above the water surface and in some plants adventitious 'water-roots' were also observed after 20 d of flooding. These structures were not observed in the gallery forest species *S. klotzchyana* and *H. courbaril*. The development of the cerrado species *K. coriacea* and *P. marginatum* was markedly affected by flooding, no new leaves appeared, the expansion of the existing ones was inhibited and some plants lost their cotyledons.

(2) Aerobic and anaerobic respiration

After 1 month of flooding both gallery forest species presented a significant drop in oxygen uptake, whereas the roots of *C. speciosa* (dry forest) and *P. marginatum* (cerrado) presented a significant increase in oxygen uptake. One month of flooding had no effect upon the respiratory metabolism of the cerrado species *K. coriacea* (Fig. 2).

When ethanol is the sole end product of anaerobiosis there should be an equimolar production of CO_2 and ethanol. If glycolysis is at the same rate, the CO_2 output per molecule of glucose metabolized, should be a third of that produced aerobically. Since all values of $Q\text{CO}_2^N/Q\text{CO}_2^{\text{air}}$ in Fig. 3 are higher than 0.33 all species showed an acceleration of glycolysis when incubated in anaerobic conditions (Pasteur Effect). Only detached roots of flooded *S. klotzchyana* presented an acceleration significantly higher than that observed in the roots of control plants (Fig. 3).

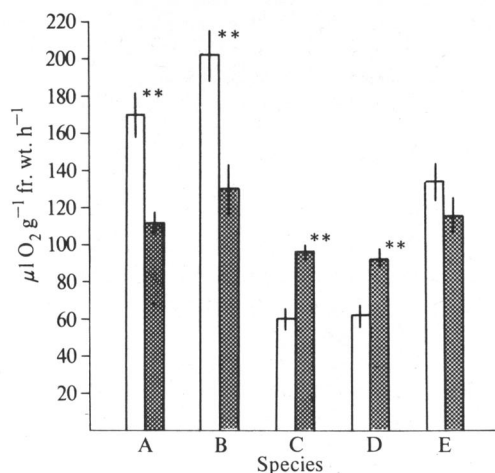


FIG. 2. Oxygen uptake by the roots of 3-month-old plants (□ control) subsequently flooded (▨) for 1 month. A—*S. klotzchyana*; B—*H. courbaril* var. *stilbocarpa*; C—*C. speciosa*; D—*P. marginatum*; E—*K. coriacea*. (Four replicates for each determination with each species; bars are s.e.; ** $P < 0.01$).

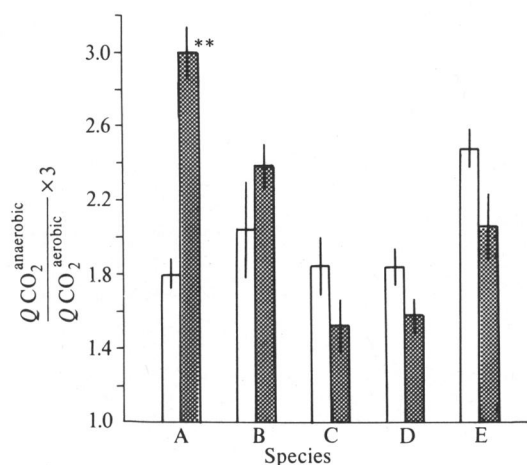


FIG. 3. Acceleration of glycolysis in roots of 3-month-old plants (□ control) subsequently flooded (▨) for 1 month when placed in anaerobic conditions. A—*S. klotzchyana*; B—*H. courbaril* var. *stilbocarpa*; C—*C. speciosa*; D—*P. marginatum*; E—*K. coriacea*. (Four replicates for each determination with each species; bars are s.e.; ** $P < 0.01$).

The rate of ethanol produced by detached roots of control plants incubated in anaerobic conditions is directly correlated with the level of the aerobic respiration (Fig. 4). This means that independent of the response observed when the whole plant is flooded, detached roots of a species with a high aerobic respiration rate present a high rate of ethanol production when placed under anaerobic conditions.

(3) Metabolic products

Ethanol was the only product that increased significantly on flooding in the gallery forest species *S. klotzchyana* (Fig. 5). The levels of malate, lactate and succinate were stable

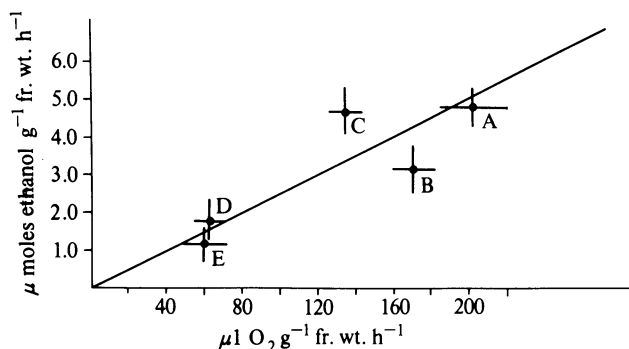


FIG. 4. Correlation between the rate of aerobic respiration and the rate of ethanol produced by roots of control plants placed in anaerobic conditions. A—*H. courbaril* var. *Stilbocarpa*; B—*S. klotzchyana*; C—*K. coriacea*; D—*P. marginatum*; E—*C. speciosa* (Four replicates for each determination with each species; bars are s.e.; $r = 0.94$, $P < 0.01$).

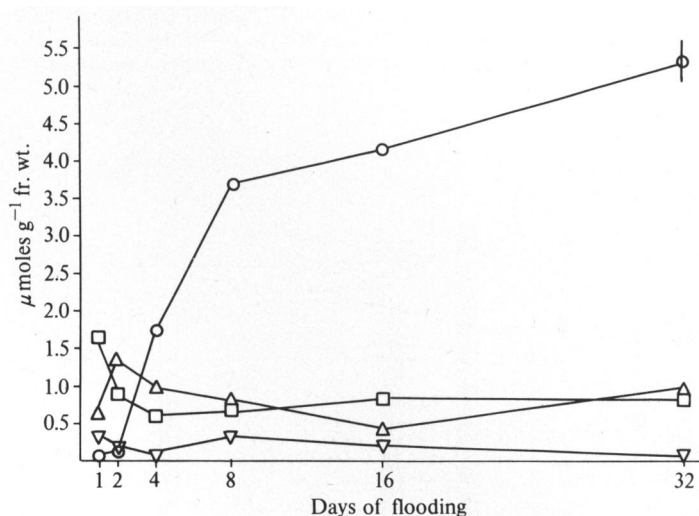


FIG. 5. Accumulation of glycolytic and related metabolites in the roots of 3-month-old plants of the gallery forest species *S. klotzchyana*. ○ Ethanol (+10; bar is l.s.d. for $P < 0.01$); □ Malate (n.s.); △ Lactate (n.s.); ▽ Succinate (n.s.)

during the treatment, while ethanol accumulated progressively, reaching $53 \mu\text{mol g}^{-1}$ fresh weight after 1 month of flooding (Fig. 5).

In the other gallery forest species, *H. courbaril*, there was no significant change in the level of ethanol throughout the experiment (Fig. 6). In contrast, there was a significant increase in the levels of malate, lactate and succinate after 2 d of flooding. Malate was the main product accumulated in this period and its total amount was four times higher than lactate or succinate (Fig. 6).

The levels of malate, ethanol and lactate rose until the fourth day of flooding in *C. speciosa* (Fig. 7). Subsequently the levels of malate and lactate dropped, while the level of ethanol was stable until the end of the experiment (Fig. 7). There was no significant change in the level of succinate throughout the experiment.

Ethanol is the main product accumulated by both cerrado species, *P. marginatum* (Fig. 8) and *K. coriacea* (Fig. 9). However, after 1 month of flooding the amount accumulated in both species is about five times lower than that obtained for *S. klotzchyana*, a flood tolerant

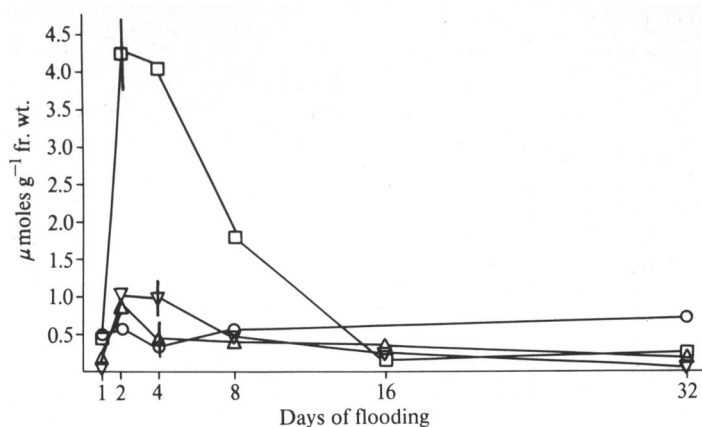


FIG. 6. Accumulation of glycolytic and related metabolites in the roots of 3-month-old plants of the gallery forest species *H. coubaril* var *stilbocarpa*. ○ Ethanol (n.s.), □ Malate (bar is l.s.d. for $P < 0.05$); △ Lactate (bar is l.s.d. for $P < 0.05$); ▽ Succinate (bar is l.s.d. for $P < 0.05$).

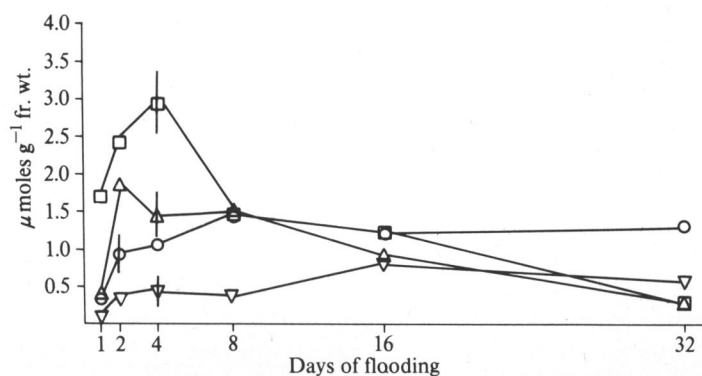


FIG. 7. Accumulation of glycolytic and related metabolites in the roots of 3-month-old plants of the dry forest species *C. speciosa*. ○ Ethanol (bar is l.s.d. for $P < 0.05$); □ Malate (bar is l.s.d. for $P < 0.05$); △ Lactate (bar is l.s.d. for $P < 0.05$); ▽ Succinate (bar is l.s.d. for $P < 0.05$).

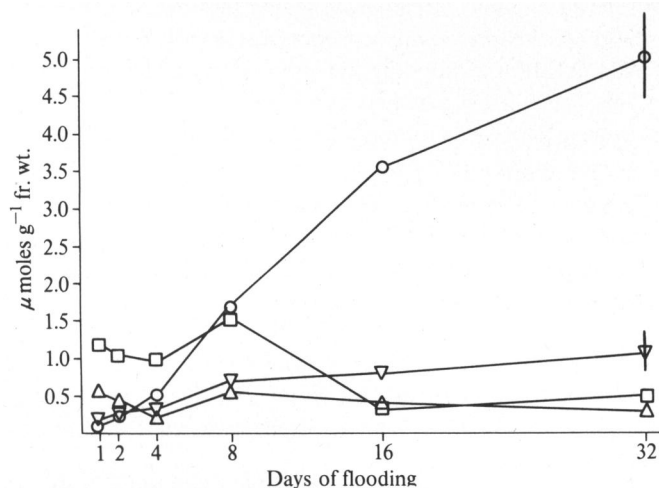


FIG. 8. Accumulation of glycolytic and related metabolites in the roots of 3-month-old plants of the cerrado species *P. marginatum*. ○ Ethanol (± 2 ; bar is l.s.d. for $P < 0.05$); □ Malate (n.s.); △ Lactate (n.s.); ▽ Succinate (bar is l.s.d. for $P < 0.05$).

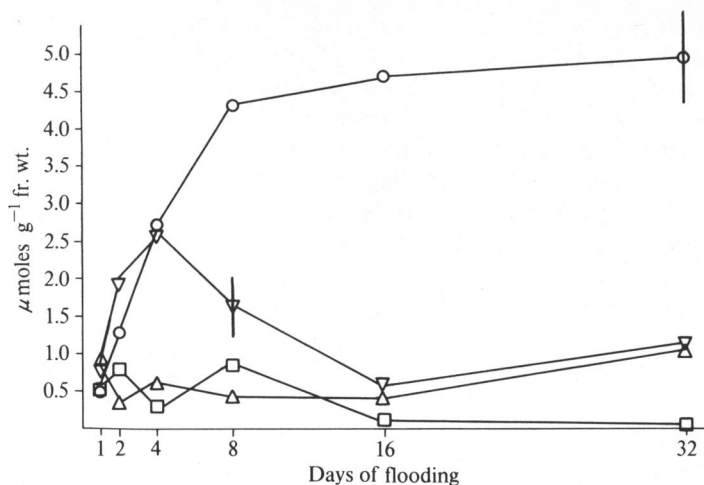


FIG. 9. Accumulation of glycolytic and related metabolites in the roots of 3-month-old plants of the cerrado species *K. coriacea*. ○ Ethanol (± 2 ; bar is l.s.d. for $P < 0.05$); □ Malate (n.s.); △ Lactate (n.s.); ▽ Succinate (bar is l.s.d. for $P < 0.05$).

species. In *P. marginatum* there was a progressive accumulation of succinate (Fig. 8), while in *K. coriacea* the level of succinate increased significantly until the fourth day of flooding, after which it dropped (Fig. 9).

DISCUSSION

Studying the effect of flooding on one tropical species, Keeley (1979) demonstrated that the metabolic responses did not agree with the general pattern observed by Crawford (1978) for temperate flood-tolerant species. The results obtained with the five species in this investigation are sufficient to show that there is a considerable degree of variation in response to flooding in tropical trees.

In the two non-flood-tolerant species, *K. coriacea* and *P. marginatum*, the response is similar to that observed already in temperate plants that are sensitive to flooding (Crawford, 1978). In both these species there was a progressive rise in the ethanol concentration in the roots with increased duration of flooding. As pointed out previously (Barclay and Crawford, 1982), no direct link has been found between ethanol and flood sensitivity, but merely that ethanol accumulation in roots is commonly found in flood-intolerant species. Neither of these flood-intolerant species showed any change in the malic or lactic acid levels in the roots when flooded. The increase in the level of succinate, particularly in *K. coriacea*, may be due to an early inhibition of succinate dehydrogenase by the high levels of CO_2 (Bendall, Ranson, and Walker, 1960).

Contrasting with the flood-intolerant cerrado species a diversity of responses were observed in flood-tolerant trees. The temporary peaks of the measured organic acids found in *H. courbaril* and *C. speciosa* are very similar to changes that take place in germinating seeds where initial periods of anaerobiosis appear to be linked either with the accumulation of lactic acid (Sherwin and Simon, 1969) or lactic acid, malic acid and ethanol as found in chick pea (Aldasoro and Nicolas, 1980).

In *H. courbaril* the initial accumulation of organic acids was followed by a drastic drop in the respiratory metabolism of the roots. As this reduction is real and not due to the presence of dead material in the samples, it suggests a low aerobic metabolism using oxygen diffused

from the aerial part. The control of aerobic respiration is probably not due to the amount of oxygen available (Armstrong and Gaynard, 1976) as oxygen only becomes limiting to aerobic respiration at very low concentrations. However, there are other possible regulators, such as high concentrations of CO_2 in the flooded soil environment.

The low frequency of *H. courbaril* in the gallery forests and its restriction to the areas under water only at the height of the flooding season, so that the trees are not water-logged for long periods (Gibbs and Leitão Filho, 1978), suggests that although the flooding tolerance mechanism developed by this species enables it to survive in this environment it is not as effective as the one developed by *S. klotzchyana*.

The correlation between respiration rate and ethanol production under anoxia by detached roots (Fig. 4) contrasts with the behaviour of the flooded roots of intact plants of *H. courbaril* (Fig. 6). This illustrates the difficulty of correlating the complex mechanism of flooding tolerance with results obtained with isolated organs. A basic reason for the different responses to what seems to be the same stress may be the speed of environmental change. The gradual change in the flooded soil environment, added to the possibility of oxygen diffusion from the aerial part to the root, contrasts with the immediate exposure to anoxia in the Warburg flask.

C. speciosa was the only species to present morpho-anatomic changes induced by flooding. The development of hypertrophic lenticels appears to be synchronized with changes in the metabolism of the roots, because by the time these structures appeared there was a stabilization of the level of ethanol and a drop in the levels of malate and lactate (Fig. 7). Hypertrophic lenticels not only facilitate a better aeration of the root system (Armstrong, 1979; Chirkova, 1978; Hook and Scholtens, 1978; Keeley, 1979), but allow volatile products like ethanol and acetaldehyde to diffuse upwards (Chirkova and Gutman, 1972). The drop in the level of malate and lactate after 4 d of flooding was similar to that observed in *H. courbaril*, and again it seems to be correlated with the development of a long-term response to the stress.

To trace the typical environment of *C. speciosa* is not easy because it is largely used as an ornamental species. It probably was an original constituent of the extensive forest that once covered the interior of the state of São Paulo before the expansion of coffee plantations. Nevertheless, its ability to grow while flooded suggests that its absence from the gallery forest is due to other factors than its ability to withstand flooding.

S. klotzchyana does not conform to the pattern of the other two flood-tolerant species in avoiding internal ethanol accumulation in the roots (Fig. 5), but behaves in the manner of the flood-intolerant cerrado species. The strategy of increasing glycolysis in response to flooding has been observed in various flood-tolerant species (Grineva, 1963; Hook *et al.*, 1971; Keeley 1978, 1979; Keeley and Franz, 1979). These authors considered this acceleration as an adaptative response because in the absence of aerobic respiration alcoholic fermentation as a compensatory energy source depends on an acceleration of glycolysis (Hochachka and Somero, 1973). The significant increase in the Pasteur Effect (Fig. 3) after 1 month of flooding shows that this species possesses both a short- and a long-term response to anoxia.

The substitution of the root system, as a long-term response, could explain the absence of metabolic and morpho-anatomic adaptations to avoid the accumulation of ethanol during the initial period of flooding. The development of morphologically distinct roots as a response to flooding has been observed in various species (Bryant, 1934; Hook, Brown, and Kormanik, 1970; Gill, 1975). The root system of *Nyssa sylvatica* var. *biflora* (Keeley, 1979) is entirely substituted after 1 year of flooding. Whereas the original root system accelerated alcoholic fermentation when flooded, the new root system had a better aeration and 'the hypoxic conditions of the soil are avoided and the rates of ethanol production similar to those of drained plants' (Keeley, 1979). Although *S. klotzchyana* would hardly ever be exposed to 1

year of flooding, periods longer than 1 month are common in its natural habitat. This is an aspect that will be considered in future experiments.

The fact that *S. klotzchiana* is a dominant species in flood prone areas (Klein, 1963; Gibbs and Leitão Filho, 1978) demonstrates that whatever the mechanism it has developed the strategy is effective and represents a strong competitive advantage.

CONCLUSIONS

From the results presented it seems clear that during the process of evolution various strategies developed to enable plants to occupy flood prone areas. It is necessary to enlarge the number of tropical species studied before any general trends can be established.

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