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ANATOMICAL ALTERATIONS IN PLANTS OF
Chorisia speciosa A. St.- Hil. SUBMITTED TO FLOODING

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SUMMARY

An experiment was carried out in order to study the mor-pho-anatomical responses of plants of Chorisia speciosa *to flooding. Plants were maintained in well-drained and flooded soils for 45 days. The flooded plants grew less than the control and formed a great number of hypertrophied lenticels. Flooding caused death of part of the original roots and the remaining roots exhibited low regeneration capacity. The stem base of* flooded plants showed a thicker cortex, narrower vessel members and a lower number of sclerenchyma bundles than the control. In the transition region of flooded plants hypertrophied lenticels, hair and root primordia were observed. Although vegetative growth was reduced in flooded plants, the species presented morpho-anatomical plasticity, which could contribute to its tolerance to flooding.

RESUMEN

Con el fin de estudiar las respuestas morfoanatómicas de C. Speciosa, *plantas juveniles fueron cultivadas por 45 días en suelo drenado y suelo anegado. El anegamiento provocó la muerte de parte de las raíces originales habiendo baja regeneración de nuevas raíces. La base del tallo de las plantas anegadas presentó una corteza de mayor espesor, elementos vasculares con menor diámetro, un número menor de haces* esclerenquimáticos y presencia de lentículas hipertrofiadas, en comparación con los controles. En la región de transición de las plantas anegadas se observaron lentículas hipertrofiadas, vellocidades y primordios de raíces. Aunque las plantas anegadas tuvieron menor crecimiento, la especie presentó plasticidad morfoanatómica, lo que pudo haber contribuido a su tolerancia al anegamiento.

Introduction

Energetic levels generally decrease in plants submitted to flooding (Davies *et al.*, 1987), and a rapid reduction in carbohydrate reserves (Saglio *et al.*, 1980), cytoplasmic pH changes (Davies *et al.*, 1987) and ultrastructural changes (Vartapetian, 1991) take place. Nutrient uptake (Bianchini, 1998; Pimenta, 1998) and photosynthesis (Pimenta, 1998; Davanso-Fabro, 1998; Fernández *et al.*, 1999) may be reduced because of these and other changes.

Some plant species have developed tolerance mechanisms for oxygen shortage during evolution. This tolerance may be obtained by structures that improve gas exchange (Armstrong *et al.*, 1994). Among the morpho-anatomical modifications that occur in plants submitted to flooding, the development of hypertrophied lenticels (Yamamoto *et al.*, 1995; Kolb *et al.*, 1998; Medri *et al.*, 1998; Pimenta *et al.*, 1998), aerenchyma formation in the roots and the stem-base (Jackson, 1989; Yamamoto *et al.*, 1995; Davanso-Fabro *et al.*, 1998,) and adventitious rooting can be emphasized (Yamamoto *et al.*, 1995). Such modifications may assist in aeration of roots and in oxidation of the rhizosphere. However, studies done on tropical tree species have shown high variation in the morpho-anatomical response (Pimenta *et al.*, 1996; Davanso-Fabro *et al.*, 1998; Kolb *et al.*, 1998; Medri *et al.*, 1998). Thus, morpho-anatomical modifications are very important for some species to tolerate flooding. In other species, this tolerance is more related with metabolic adaptation (Moon *et al.*, 1993).

Many areas on the planet suffer flooding damage and the recuperation of these damaged areas with flood-resistant plants is under intense research (Blom and Voesenek, 1996). Detailed attention should be given to the diversity of flooding tolerance mechanisms in plants (Crawford and Bländle, 1996) if the preservation of biodiversity in these areas is the main aim of this research. Because tropical regions have

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KEY WORDS / *Chorisia speciosa* / Flooding / Anatomical Alterations / Riparian forest /

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RESUMO

Objetivando estudar as respostas morfo-anatômicas de C. speciosa, *plantas jovens foram cultivadas em solo drenado e em solo alagado por 45 dias. O alagamento provocou morte de parte das raízes originais, havendo baixa regeneração de novas raízes. A base do caule das plantas alagadas apresentou córtex mais espesso, elementos de vaso com menor diâmetro, menor número de feixes esclerenquimáticos e presença de lenticelas* hipertrofiadas, quando comparadas às plantas-controle. Na região de transição das plantas alagadas foram observados lenticelas hipertrofiadas, pêlos e primórdios de raízes. Embora tenha sido menor o crescimento nas plantas alagadas, a espécie apresentou plasticidade morfo-anatômica, o que pode ter contribuído para sua tolerância ao alagamento.

a greater diversity of environments subject to flooding (Joly, 1991), tropical plants may have a greater diversity of tolerance strategies to flooding compared to plants from temperate regions. However, mechanisms of flood tolerance have been studied mostly in herbaceous species from temperate regions (Mazzoni-Viveiros and Luchi, 1989).

Chorisia speciosa A. St.-Hil. (Bombacaceae) is a selective hygrophyte tree species (Santos, 1967) found in riparian and seasonal semideciduous forests. Plants of this species had accelerated alcoholic fermentation with increased alcohol dehydrogenase activity (ADH) and ethanol production was higher at the beginning of flooding, while the ethanol content detected in the roots became stable after eight days of flooding (Joly and Crawford, 1982).

Considering the relationship between morpho-anatomical modifications and the capacity to tolerate flooding, we raised the question: which morpho-anatomical alterations occur in plants of *Chorisia speciosa* submitted to flooding?

Material and Methods

Four hundred seeds of *C. speciosa* were placed to germinate in a greenhouse after mechanical scarification, in four PVC boxes containing sand as substrate. The seedlings were irrigated with 10% Hoagland solution every two days.

After one month, the plants from two boxes were flooded (F) for 45 days, keeping the water level at 2 cm above the substrate, while the plants in the other two boxes were maintained in well-drained conditions (D).

Dry biomass was determined in 15 plants from each treatment to assess the growth and development of *C. speciosa* after 45 days' flooding. The roots and shoots of these plants were separated and placed in a drying chamber at 70ºC for 72 hours, then weighed on a semi analytic balance.

Segments from the stem base, collected 2 cm above the substrate, and from the transition region were used for the anatomical study. The samples were fixed in 50% FAA, dehydrated in an ethanol-xylol series and embedded in paraffin (Johansen, 1940) in a vacuum chamber at 60ºC. Transverse sections 13 µm thick were stained with astra blue - basic fuchsin and mounted in Canadian balsam (Luque *et al.*, 1996).
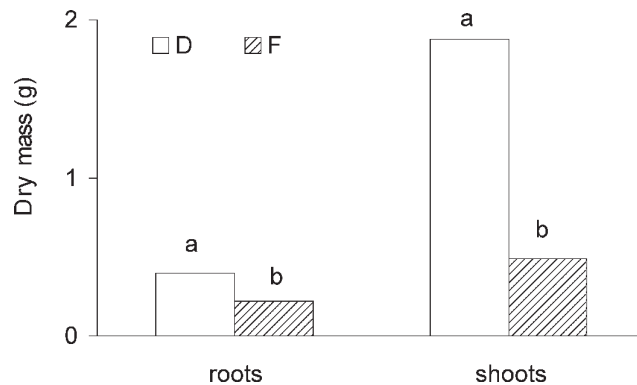

Figure 1. Dry mass of roots and shoots of plants of *C. speciosa* grown at well-drained condition (D) and flooded for 45 days (F). Bars followed by different letters differ statistically by the Tukey test (P ≤ 0.05; n = 15).

Segments from the base of the control plants and from flooded plants were collected to study the vessel elements of the xylem. These segments were treated with Jeffrey's solution (1:1 chromic acid and nitric acid) in hermetically sealed flasks and kept in a chamber at 60ºC for four days (Johansen, 1940). The macerate obtained was stained with basic fuchsin.

All the microscopic measurements were carried out with a micrometric eyepiece, using five plants, one slide per plant and a hundred cells.
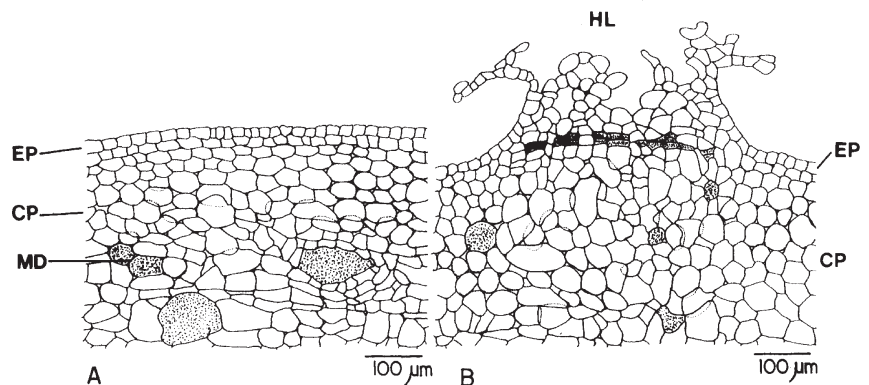

Figure 2. Transverse section of the cortical region of the stem base of plants of *C. speciosa* grown at well-drained condition (A) and flooded for 45 days (B). CP: cortical parenchyma; EP: epidermis; HL: hypertrophied lenticel; MD: mucilage ducts.

The histological drawings were done using a zoom drawing tube. The gravimetric method (Medri, 1980) was used to assess the percentage of intercellular spaces.

Results

After 45 days of flooding, root and shoot dry mass were significantly smaller than in the control plants (Figure 1). Adventitious roots and the regeneration of new superficial lateral roots were observed on some of the plants.

While no hypertrophied lenticels were found in the stem base of control plants, these structures were abundant in the stem base in flooded plants (Figure 2).

The stem base of control plants had an early secondary structure, because the vascular cambium was already differentiated (Figure 3). Comparatively, the flooded plants had epidermal cells with greater radial diameter (Table I) and thicker cortex (Figure 4, Table I), because of a greater number of cell layers (Figure 3) and a larger cell size (Table I). Flooded plants had a greater area occupied by cortex, a smaller area occupied by phloem and xylem (Figure 4) and a smaller number of sclerenchyma bundles (Figure 5) than control plants. No differences were observed in the number (Figure 5) and the length (Table I) of the vessel elements of the stem base of flooded plants compared with the control plants. However, the diameter of these elements was significantly smaller in the flooded plants (Table I).

Phellogen and vascular cambium were observed in the transition region of 75-days-old plants. Hypertrophied lenticels and longitudinal cracks (data not shown), hairs (Figure 6) and root tips (Figure 7) were found in this region in the flooded plants. The cortical cells were larger and the cortex thicker in the transition region of flooded plants compared with the control plants (Table II). How-

TABLE I
COMPARED ANATOMY OF THE STEM BASE OF CONTROL AND FLOODED PLANTS OF *C. speciosa.*

Assessed parameters	Control (µm)	Flooded (µm)
Radial diameter epidermal cells	17.62 b	24.01 a
Cortex thickness	449.80 b	677.30 a
Radial diameter cortical parenchyma cells	33.10 b	37.30 a
Length vessel elements	274.10 a	240.50 a
Radial diameter vessel elements	51.70 a	26.40 b

The means followed by different letters on a row differ statistically by the Tukey ($P \leq 0.05$) test.
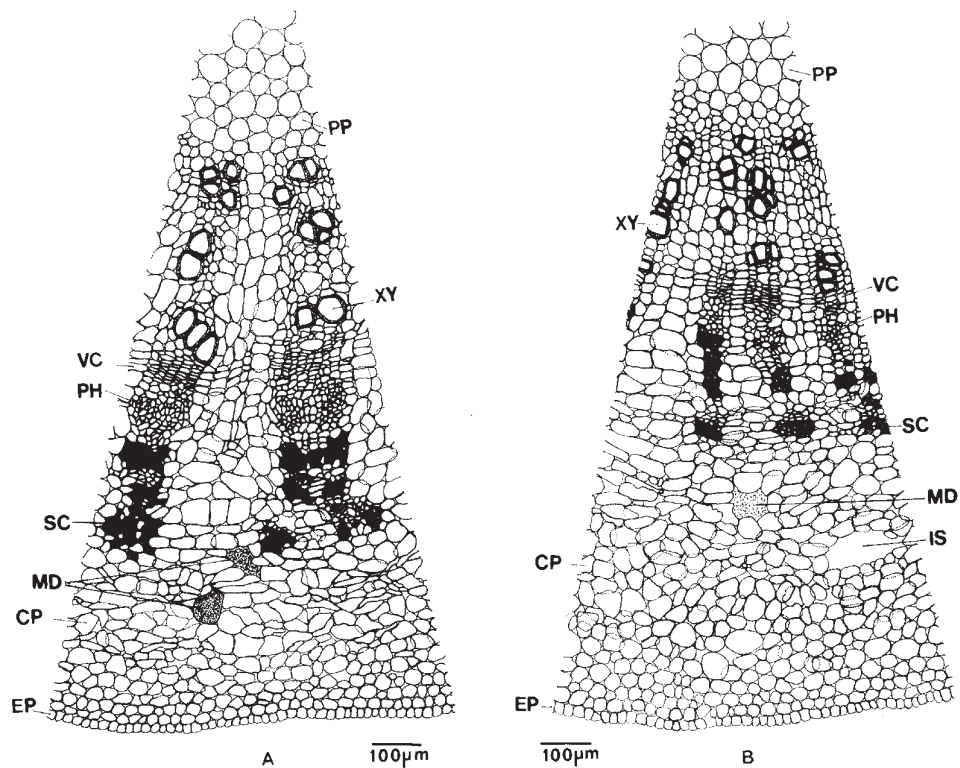

Figure 3. Transverse section of the stem base of plants of *C. speciosa* grown at well-drained conditions (A) and flooded for 45 days (B). CP: cortical parenchyma; EP: epidermis; IS: large intercellular space; MD: mucilage ducts; PH: phloem; PP: pith parenchyma; SC: sclerenchyma; VC: vascular cambium; XY: xylem.

TABLE II
COMPARED ANATOMY OF THE TRANSITION REGION OF CONTROL AND FLOODED PLANTS OF *C. speciosa.*

Assessed parameters	Control (µm)	Flooded (µm)
Radial diameter cortical parenchyma cells	43.8 b	46.3 a
Cortex thickness	638.0 b	755.0 a
Total diameter	2,169.0 a	2,471.0 a

The means followed by a different letter on a row differ statistically by the Tukey ($P \leq 0.05$) test.
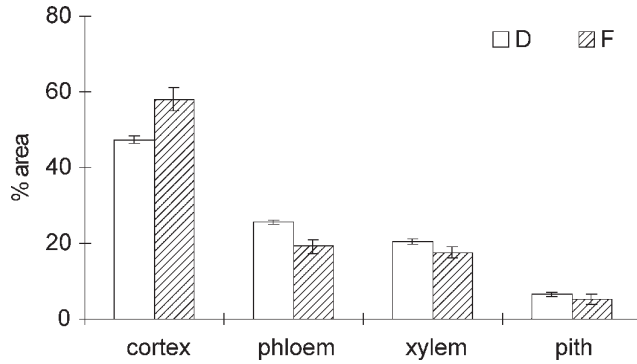
Figure 4. Relative area occupied by the different tissues of the stem base of *C. speciosa* plants grown at well-drained conditions (D) and flooded for 45 days (F). The values are means $\pm$ SE (n = 5).
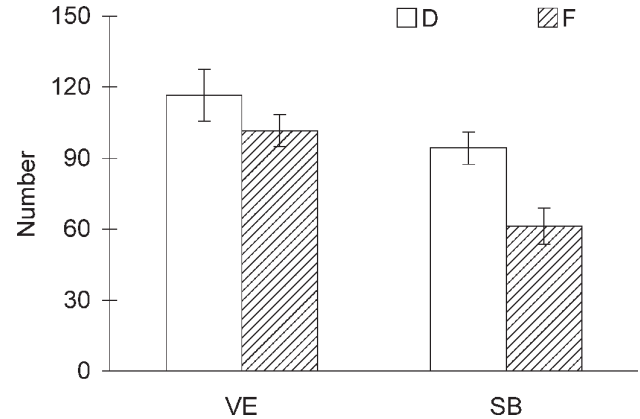

Figure 5. Number of vessels elements (VE) and sclerenchyma bundles (SB) in transverse section of the stem base of plants of *C. speciosa* grown at well-drained condition (D) and flooded for 45 days (F). The values are means $\pm$ SE (n = 5).

ever, there was no difference in the thickness of this region when the two treatments were compared (Table II).

Many mucilage ducts were found in the stem base cortex of the control and flooded plants, the ducts being smaller in the flooded plants (Figure 2).

Discussion

Growth and development of young plants of *C. speciosa* were negatively affected by flooding, similarly to several other neotropical tree species such as *Jacaranda puberula* (Pimenta *et al.*, 1996), *Peltophorum dubium* (Medri *et al.*, 1998), *Sebastiania commersoniana* (Kolb *et al.*, 1998), *Chrysophyllum gonocarpum* (Bianchini, 1998) and *Campomanesia xanthocarpa* (Pimenta, 1998).

The small root dry mass of flooded plants of *C. speciosa* was the result, in part, of the deterioration and low regeneration of the original root system, which possibly resulted in reduction of the leaf water potential as observed in flooded plants of *C. speciosa* by Pimenta *et al.* (1998). Smaller root system also may affect nutrient uptake and photosynthesis in these plants. Reduction in nutrient uptake was observed in flooded plants of *Chrysophyllum gonocarpum* (Bianchini, 1998) and *Campomanesia*

xanthocarpa (Pimenta, 1998). Flooding also affected photosynthesis in several tropical tree species (Davanso-Fabro, 1998; Lobo-Faria, 1998; Pimenta, 1998; Fernandez *et al.*, 1999).

Inhibition of the Krebs cycle and the respiratory chain are the most commonly reported plant reactions to flooding (Kozlowski, 1984), resulting in less energy production, which may affect various processes in the plants. The lesser growth and development in the flooded plants of *C. speciosa* may be connected to a lower energetic content.

In plants grown in well-drained soils, the original lateral roots are not effectively adapted to withstand flooding. They die during hypoxia and new superficial roots that are more porous and with a greater diameter than original roots are formed in flood-tolerant species (Lobo and Joly, 1995; Kolb *et al.*, 1998). These roots normally grow in the transition region and stem base, enabling a better exploitation of the more aerated soil surface. No significant increase in root porosity was found in *C. speciosa*, probably because of the slow root regeneration in this system. However, the occurrence of hypertrophied lenticels enables greater oxygen entrance to the plant, and small in-

creases in the porosity improve the aeration of the root system (De Willigen and Van Nordwijk, 1989). Joly and Crawford (1982) demonstrated the function of the hypertrophied lenticels in oxygen diffusion to the root system in *C. speciosa*, as did Pimenta *et al.* (1998) in *Peltophorum dubium.*

Flooding may increase the auxin levels at the stem base (Visser *et al.*, 1995), and may affect the extension of the cortex cell walls (Cleland, 1995) resulting in larger cells, as observed in *C. speciosa*.
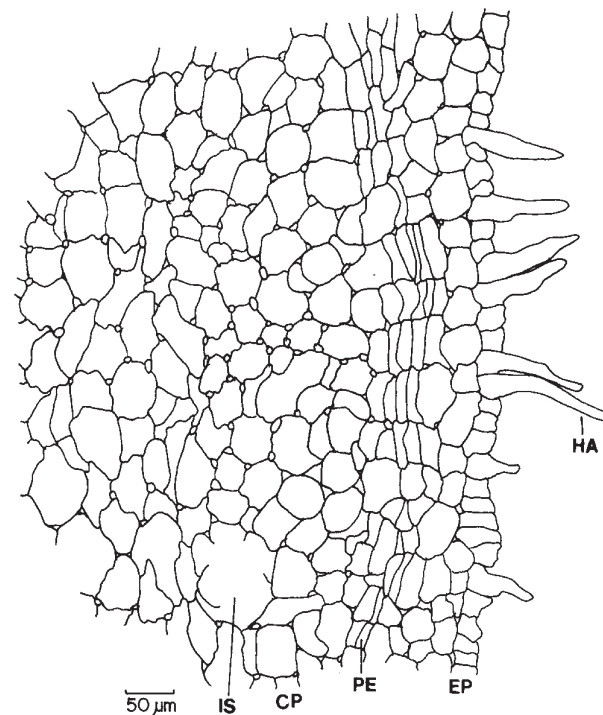

Figure 6. Transverse section of the cortex from the transition region of plants of *C. speciosa* grown under flooding for 45 days. CP: cortical parenchyma; EP: epidermis; HA: hairs; IS: large intercellular space; PE: phellogen.

The rearrangement of these larger cortex cells may result in an increase in the air space between the cells, and may contribute to greater oxygen diffusion to the roots. Hypertrophy and hyperplasia of the stem base cortex were observed in *Jacaranda puberula* (Pimenta *et al.*, 1996), *Peltophorum dubium* (Medri *et al.*, 1998) and *Sesbania virgata* (Davanso-Fabro *et al.*, 1998).

The mechanisms involved in the induction of adventitious root development, lenticel hypertrophy and aerenchyma formation are linked to hormone level alterations caused by flooding. The increased ethylene level in plants submitted to this stress is probably related to lenticel hypertrophy (Medri *et al.*, 1998) and aerenchyma formation (Yamamoto *et al.*, 1995; Medri *et al.*, 1998). In the case of *C. speciosa*, lenticel hypertrophy occurred in all the plants and only some individuals formed adventitious roots. These observations suggest that this species has genetic variability for individual sensitivity to hormonal alterations. However, the occurrence of root primordia in the transition region of flooded plants suggests that the duration of the experiment was relatively short for this response. The number of adventitious roots may increase with extended experimental time.

Formation of hairs in the transition region of *C. speciosa* may be important because they increase the absorption surface. Ethylene also acts as a positive regulator in the hair formation on the roots of many species (Abeles *et al.*, 1992; Doland *et al.*, 1994). Davanso-Fabro (1998) observed formation of many hairs on the superficial lateral root bases of *Tabebuia avellanedae* submitted to flooding, and considered that the new superficial root and hair formation under hypoxia partly recovered the absorption capacity of these plants under stress.

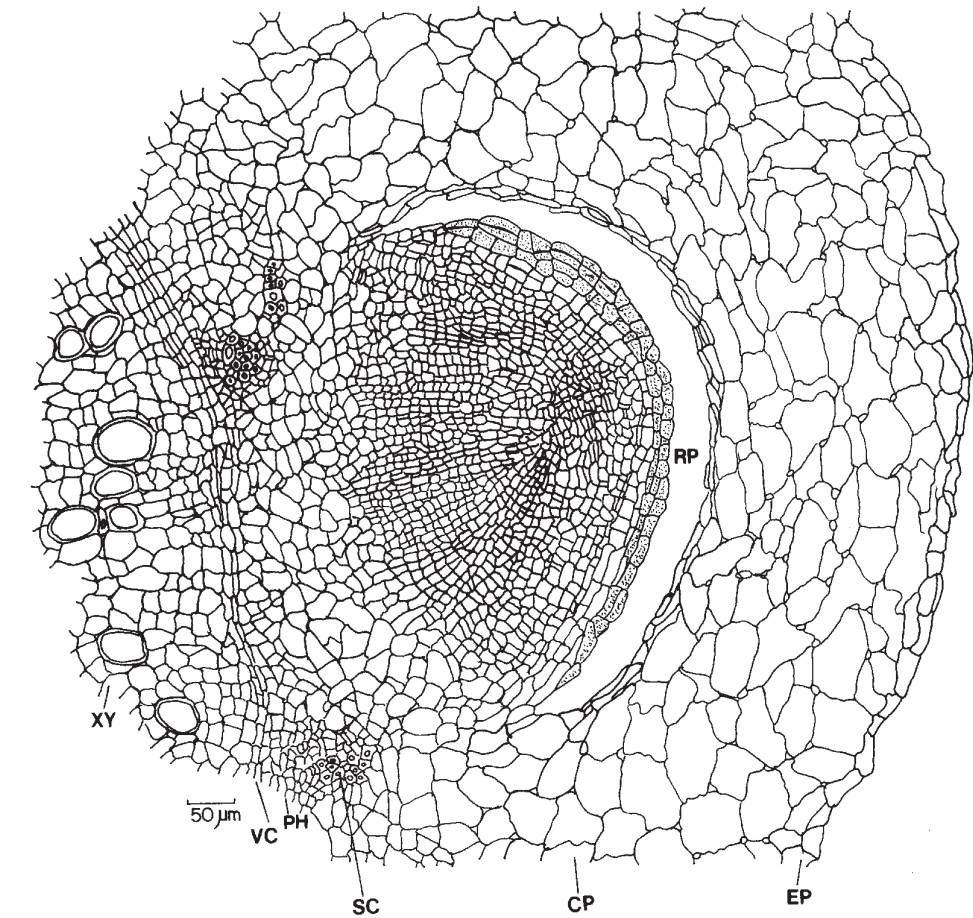Flooding affected the vessel elements in *C. speciosa*. This

Figure 7. Transverse section of the transition region of plants of *C. speciosa* grown under flooding for 45 days. CP: cortical parenchyma; EP: epidermis; PH: phloem; RP: root primordium; SC: sclerenchyma; VC: vascular cambium; XY: xylem.

was also observed in *Sebastiania commersoniana* (Kolb *et al.*, 1998). According to Zimmermann (1978) narrow vessels elements with low conductance are extremely important in unfavorable environmental conditions, such as in cases of water stress. The possibility of embolism occurrence is reduced when these elements are narrow.

Analysis of the *C. speciosa* anatomic data suggests that flooding reduced the cambial activity and reduced cell wall lignification. This strategy may enable the plants to use the available energy in other processes such as the production of hypertrophied lenticels, which allow them to tolerate stress.

Survival of plants under flooded conditions may be more important than growth maintenance. Although there was a significant decrease in the growth of *C. speciosa*, no plant died during flooding, indicating that the morpho-anatomical modifications are important for this species in tolerating stress periods. Modifications that stand out among those observed include the increase in cortex cell size and lenticel hypertrophy which could facilitate O_2 absorption and diffusion to the root system, while the decrease in the vessel element diameter may restrict embolism.

The metabolic responses shown by Joly and Crawford (1982) and the morpho-ana-tomical responses shown here for plants of *C. speciosa* under flooding corroborate the idea that, in this species, there is an interaction of morpho-anatomical and physiological responses that enable them to survive in environments subject to periodic flooding. However, other factors are involved in the distribution of this species in the riparian forest, because it is not frequently found in periodically flooded areas.

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