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Tabebuia avellanedae Lor. ex Griseb. (Bignoniaceae) Submitted at the Flooding and the "Ethrel" and Silver Nitrate Application

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ABSTRACT

Three-month-old Tabebuia avellanedae *Lor. ex Griseb. (Bignoniaceae) plants cultivated in the greenhouse were submitted to 56 days of flooding and to "Ethrel" and silver nitrate applications to find out it's capacity for morphological and physiological modifications to survive under flooding conditions and at which degree such responses were correlated with alterations in the ethylene level. Flooding and the "Ethrel" application caused growth reduction and epinasty in* T. avellanedae *and the application of silver nitrate lessened some these symptoms. Certain symptoms shown during flooding by this species and its ability to develop structures which lessen hypoxia effects, such as stem fissures and hypertrophied lenticels in the roots, modifications which enable the species to adapt to short flooding periods, could be related to increases in the ethylene concentration in the plant tissues.*

Key words: flood tolerance, "Ethrel", *Tabebuia avellanedae*

INTRODUCTION

The persistence of meristems and the plasticity of cell development create options for the morphological and physiological readjustments in the plant life. Allied to the close link between form and function, they relate the hormonal action with survival capacity to stress (such as flooding). The latter condition reduces oxygen availability absorbed by roots.

Species vary in their response to hypoxia conditions during flooding and effects may change according to age of plant and environmental conditions (Ernst, 1990). In many species flooding causes changes such as growth reduction with low production of biomass (Marques et al., 1996; Kolb et al., 1998; Medri et al., 1998), epinasty, chlorosis, (Kuo and Chen, 1980; Sena-Gomes and Kozlowski, 1988; Pimenta et al., 1994), abscission (Clemens et al., 1978; Yamamoto and Kozlowski, 1987) and early senescence of leaves (Serodio and Novais, 1991; Marques et al., 1996). During flooding many species produce structures that improve gaseous exchange with the environment and the internal diffusion of oxygen, such as stem fissures (Joly and Crawford, 1982; Davanso-Fabro et al., 1998), hypertrophied lenticels (Marques et al., 1996; Colli, 1998; Kolb et al., 1998; Medri et al., 1998), surface and adventitious roots (Pimenta et al., 1994; Lobo and Joly, 1995) and aerenchyma (Drew et al., 1994; Davanso-Fabro et al., 1998; Kolb et al., 1998).

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Physiological and anatomic changes in plant structure during inundation reflect changes in hormonal levels. Ethylene is considered the most important hormone in stress conditions, as during flooding (Drew et al., 1994). Jackson et al. (1985) and Brailsford et al. (1993) stated that there was a clear relationship between decrease of partial pressure of oxygen and increase of ethylene production and, consequently, the formation of aerenchyma and adventitious roots. Studies on ethylene quantification in flooded plants (Sena-Gomes and Kozlowski, 1988; Yamamoto, 1992; Yamamoto et al., 1995; Colli, 1998), application of ethylene releasing compounds, such as "Ethrel" (Yamamoto and Kozlowski, 1987; Drew et al., 1994; Medri et al., 1998), and the latter's application associated with that of inhibitors of ethylene synthesis and action, such as cobalt (Colli, 1998), suggest that ethylene is the chief releaser of symptoms and of adapting mechanisms in plants during flooding.

Since ethylene biosynthesis requires oxygen, it has been suggested that its precursor, 1-amino-cyclopropane-1-carboxylic acid (ACC), is synthesized in roots during hypoxia conditions and quickly transported to the aerial section of plants were, in aerobic conditions, it is transformed into ethylene (Bradford and Yang, 1980; Yang and Hoffman, 1984).

Since all responses originating from flooding affect plant growth, there is certainly an interaction between ethylene and other vegetal hormones (Blom et al., 1994). Lack of oxygen between the stem and the roots interferes in the descending translocation of auxins. Its accumulation may stimulate tissue hypertrophy in the region and the development of adventitious roots (Bradford and Yang, 1980). In their study on *Helianthus annuus*, Liu and Reid (1992) suggested that ethylene increases the sensitiveness of tissue for auxin. Zhang and Davies (1987) verified an increase in the concentration of abscisic acid (ABA) in the leaves of flooded plants. An increase in ABA concentration in leaves as a response to decrease in water potential during inundation would be related to the closing of stomata (Armstrong et al., 1994). However, this mechanism is still largely unknown. Growth and longevity of leaves may be impaired by a decrease in cytocynin and gibberellin supply in flooded roots (Jackson et al., 1985). Neuman et al. (1990) suggested that growth of aerial part may be more impaired by the accumulation of inhibitors such as ABA and ethylene than by the lack of cytocynin and gibberellin.

Present research concentrated on *Tabebuia avellanedae* Lor. ex Griseb. (Bignoniaceae), commonly known as "ipê-roxo" in Brazil. This species occurs from Maranhão (North state) to the south of Brazil, especially in the states of Mato Grosso do Sul and São Paulo. It occupies the upper dossel of the semi-deciduous forest of the Paraná River basin where it is extremely abundant (Lorenzi, 1992). *Tabebuia avellanedae* plants were submitted to flooding and to "Ethrel" and silver nitrate applications attempts to answer the following questions:

- Which are the morphological and/or physiological modifications that flooding and "Ethrel" and silver nitrate applications cause in *Tabebuia avellanedae?*
- Could these changes be attributed to ethylene?

MATERIALS AND METHODS

Seeds of *Tabebuia avellanedae* were removed from fruit, washed, dried and left to germinate in recipients with 700 g of wet substratum consisting of 80% soil and 20% mixture of grated grass, lime and coffee powder. Germination occurred in a nursery. After two months, some plants, selected according to their uniformity in size and development, were taken to the greenhouse. Together with the substratum they were placed in 4-L plastic pots with soil and sand in a 3:1 proportion. Experiment started a month after plant acclimatization.

On first day of the experiment, the length of the root and aerial section, number of leaves, leaf area and stem diameter at 2cm from soil (slide ruler) of 10 plants were measured. To determine leaf area, two correcting values, 0.726 and 0.376, were determined for simple and compound leaves respectively from previous length measurements, width and area of 60 leaves by the gravimetric method. Plants were then divided into leaves, stems and roots and placed in a buffer at 60° C during 72 hours to obtain constant dry weight.

Other 60 plants were divided into six groups: fc (field capacity); fcEth (field capacity with application of 2-chloro-ethyl-phosphonic acid, commercially known as "Ethrel" or "ethephon" at 150mg/L); fcAg (field capacity with application of silver nitrate at 0.02mg/L); fd (flooded, or plants in water at 2 cm from soil); fdEth (flooded with application of "Ethrel" at 150mg/L); fdAg (flooded with application of silver nitrate at 0.02mg/L). In the tratments with "Ethrel" (ethylene releaser) and silver nitrate (inhibitor of ethylene action), the leaves and stem of plants were sprayed with the solutions every 3 days.

Same parameters evaluated at the beginning of the experiment were taken for 10 plants of each group at the end of 56 days. Number of new leaves produced and the number of leaves lost by abscission were included also. Relative growth rate (RGR) was calculated for each part of the plant and for the entire plant. Formula employed: RGR = (In DWf – In DWi) / 56, where DWf is the final weight of dry matter and DWi is the initial weight of dry matter. Net assimilatory rate (NAR) was calculated too. Formula used: NAR = ((DWf – DWi) / (LAf – LAi)) x ((ln LAf – In LAi) / 56), where LAf is final leaf area and LAi is the initial leaf area.

Epinasty was determined weekly by measuring the angle between the stem and the petiole with protractor. Weekly follow up was also done to ensure possible formation of stem fissures, hypertrophied lenticels, diageotropic roots, intumescence of stems and roots and development of branches.

Statistic analysis was based on variance analysis (ANOVA) and LSD was determined by Tukey's test at $P\leq0.05$. Before statistically analyzed, data in percentage were transformed in arc-sines of root of the section.

RESULTS

Flood-submitted *T. avellanedae* plants had a reduction in RGR of root and of the entire plant in comparison to those in field capacity (Table 1). Ethrel application caused pronounced reduction of RGR in all sections of the plant, especially in the leaves. No difference was registered between plants in field capacity and in flood. In fdAg treatment there was RGR recovery in stem and a recovery trend in other parts of the plant (Table 1).

Flooding and "Ethrel" application in *T. avellanedae* plants caused NAR reduction when compared to controls (Table 1). In silver nitrate application plants of treatment fdAg had same values as flooded ones. Recovery trend of water assimilation was registered.

Table 1 - Relative growth rate (RGR) and net assimilatory rate (NAR) of *Tabebuia avellanedae* plants in field capacity (fc) and submitted to 56 days of flooding (fd) and "Ethrel" (Eth) and silver nitrate (Ag) applications.

	RGR (mg g^{-1} d^{-1})				NAR (mg dm^{-2} d^{-1})
Treatment	**Leaf**	**Stem**	**Root**	**Plant**	**Plant**
fc	0.022a	0.020c	0.029a	0.025a	0.026a
fcEth	-0.014b	0.011e	0.018b	0.008d	0.017b
fcAg	0.017a	0.017d	0.029a	0.021b	0.021b
fd	0.016a	0.022b	0.015cd	0.017b	0.017b
fdEth	-0.023b	0.012e	0.013d	0.003e	0.001c
fdAg	0.019a	0.026a	0.017bc	0.020b	0.020b

* Means separation within columns by Tukey's test ($P\leq0.05$; n= 10).

Table 2 - Length increase of shoot, root and entire plant of *Tabebuia avellanedae* plants in field capacity and submitted to 56 days of flooding and "Ethrel" and silver nitrate applications.

	Length increase (cm)	
Treatment	**Shoot**	**Root**
fc	5.85a	10.55a
fcEth	1.95c	7.50b
fcAg	3.15bc	6.15b
fd	4.10ab	0.00d
fdEth	2.45bc	0.00d
fdAg	3.20bc	0.15c

* Means separation within columns by Tukey's test ($P\leq0.05$; n= 10).

Length increase of aerial part of *T. avellanedae* was reduced in fcEth and fdEth treatments (Table 2). Plants in treatment fdAg showed values for extension growth similar to those of flooded plants. No increase in length of root was registered during flooding and in "Ethrel" application. Silver nitrate application in flooded plants caused a slight recovery of length of root.

The production of new leaves was reduced in fd and fcEth treatments in plants kept in field capacity (Fig. 1 A). Plants with fcAg and fdAg treatments registered values for leaf production similar to the controls (fc and fd). In fcEth and fdEth treatments abscission of leaves greatly increased, whereas in fcAg and fdAg treatments, there was no significant difference from controls (Fig. 1B). Leaf area of plants was reduced by flooding and by "Ethrel" application (Fig. 1 C). In silver nitrate application, however, increase in leaf area for fcAg plants was similar to that in field capacity plants. Further, decrease in leaf area of fdAg plants remained stable with regard to flooded plants.

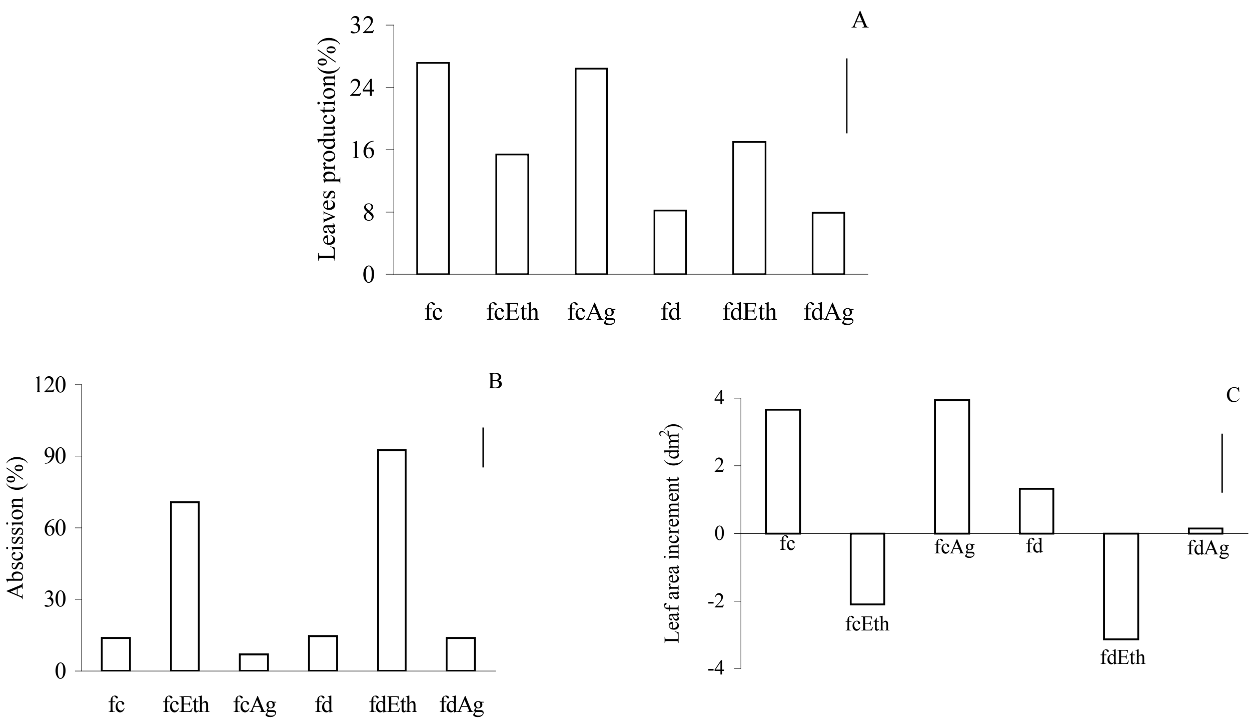

Figure 1 - Percentage of leaf production (A) and abscission (B) and increase in leaf area (C) in *T. avellanedae* plants in field capacity and submitted to 56 days of flooding and "Ethrel" and silver nitrate applications. Vertical bars represent LSD by Tukey's test ($P \leq 0.05$; n=10).

T. avellanedae plants with fd and fdEth treatments had a great increase in stem diameter when compared to that of controls (Fig. 2). Diameter values of stem in plants with treatment fdAg were similar to those of flooded ones.

Flooding didn't cause any change in leaf curvature in *T. avellanedae* leaves. There was a significant increase in leaf angle from the third week onwards in plants with fdEth treatment when compared to flooded ones. Moreover, from the seventh week plants with fcEth treatment tended towards epinasty when compared to plants in field capacity (Fig. 3). Silver nitrate application maintained epinasty in fcAg and fdAg close to that of controls.

In all treatments with flooding (fd, fdEth and fdAg), *T. avellanedae* plants developed stem fissures (Fig. 4) and hypertrophied lenticels in roots. Roots with diageotropic growth, whitish color and greatly branched, developed in the 3 treatments as from the seconding week of flooding (Fig. 4). On the other hand, original root system was less branched and with signs of necrosis when compared to fc, fcEth and fcAg plants (Fig. 5). Development of branches occurred in fcEth and fdEth treatments (Fig. 5).

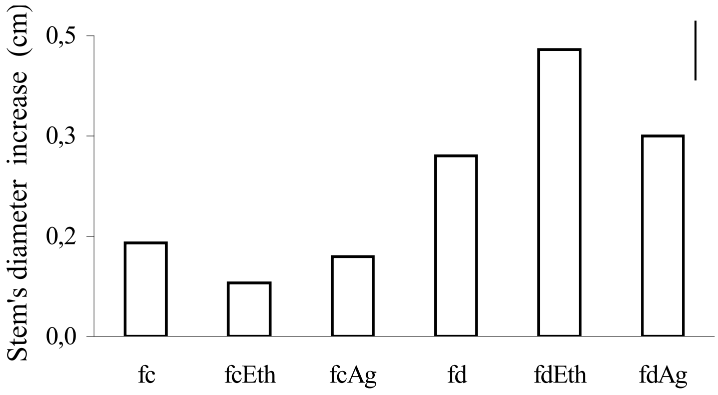

Figure 2 - Stem diameter in *T. avellanedae* plants in field capacity (fc) and submitted to 56 days of flooding (fd) and "Ethrel" (Eth) and silver nitrate (Ag) applications. Vertical bar indicate LSD by Tukey's test (P≤0.05; n=10).

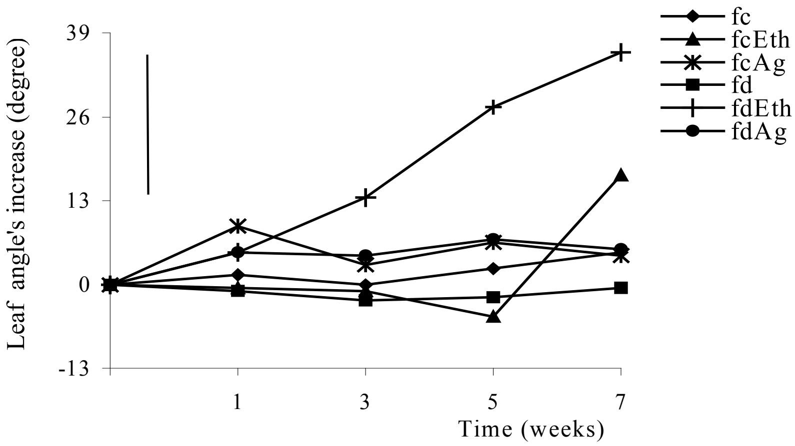

Figure 3 - Variation of leaf position in *T. avellanedae* plants in field capacity (fc) and submitted to 56 days of flooding (fd) and "Ethrel" (Eth) and silver nitrate (Ag) applications. Vertical bar indicate LSD by Tukey's test (P≤0.05; n=10).

DISCUSSION AND CONCLUSION

RGR results for *T. avellanedae* showed that "Ethrel" application promoted plant growth decrease with regard to fd treatment, whereas silver nitrate application lessened this symptom. RGR decrease of roots of flooded plants with "Ethrel" was probably a consequence of the deterioration and roots ramification inhibition. Pronounced RGR reduction in leaves of *T. avellanedae* plants with "Ethrel" application might have resulted from intense abscission in these plants. RGR reduction with "Ethrel" application was also recorded in *Coleus blumei* (Pimenta et al., 1994) and in *Peltophorum dubium* (Medri et al., 1998). Silver nitrate application with fewer symptoms by flooding has been registered by Colli (1998) in *Croton urucurana* and *Croton floribundus*.

Growth decrease in *T. avellanedae* plants, flooded and treated with "Ethrel" might have been caused by NAR decrease. Closing of stomata probably caused reduction in water assimilation, since stomata conductance of *T. avellanedae* diminished during flooding (Davanso et al., 2001).

Reduction in length increase of the shoot and chiefly of roots in *T. avellanedae* plants in fcEth and fdEth treatments has already been described for other species. It has been caused by an increase in ethylene production during hypoxia (Brailsford et al., 1993) and by ethephon application (Clemens et al., 1978; Kuo and Chen, 1980). In *T. avellanedae* results for silver nitrate application merely showed a discrete indication of ethylene involvement in length increase.

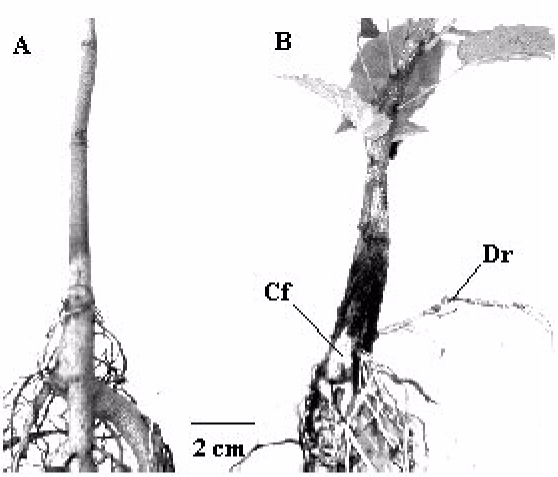

Figure 4 - *T. avellanedae* in field capacity (A) and flooded during 56 days (B), with silver nitrate application. Cf = cortical fissure; Dr = diageotropic root.

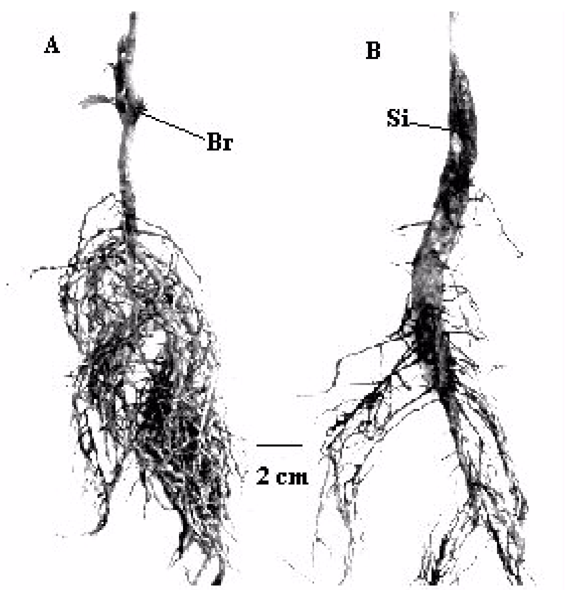

Figure 5 - *T. avellanedae* in field capacity (A) and flooded during 56 days (B), with "Ethrel" application. Si = stem intumescence; Br = branches.

Small leaf production during flooding was probably the cause of decrease in leaf area of flooded plants. In fcEth and fdEth treatments leaf area might have been reduced by a smaller production of leaves and by intense abscission due to "Ethrel" application. Many authors have registered an increase in abscission due to "Ethrel" (Pimenta et al., 1994; Colli, 1998).

Increase in diameter growth of stems of flooded plants and flooded plants with "Ethrel" was probably due to an increase in the formation of aerenchyma, since intumescent stems had a spongy aspect. Amplified aerenchyma may facilitate internal diffusion of oxygen from the aerial part to submerged regions of the plant (Wiedenroth, 1993).

It might have been provoked by ethylene (Jackson et al., 1985; Yamamoto, 1992; Brailsford et al., 1993; Drew et al., 1994). Moreover, stem hypertrophy in some species could be also the consequence of ethylene in the increase of exchange activity or even in an increase in the number and size of xylem fibers (Yamamoto et al., 1995).

It seems probable that epinasty in *T. avellanedae* may be associated with ethylene, since the increase in leaf curvature in treatment with "Ethrel" was pronounced. This occurred even though silver nitrate application in fcAg and fdAg didn't revert symptom. Low epinasty in flooded plants may be related to the fact that these plants produce fissures in the stem, hypertrophied lenticels in the roots and sufficient superficial roots to lessen the flood symptom. Stem fissures and lenticels may be also facilitating the release of ethylene in the environment (Hook and Scholtens, 1978). In fd treatment plants associated with "Ethrel" the structures produced were not sufficient to lessen the effects of "Ethrel" and of endogenous-produced ethylene. Great leaf curvature due to application of ethylene releasing compounds has been investigated in researches (Clemens et al., 1978; Kuo and Chen, 1980; Pimenta et al., 1994). The association between increase in ethylene during flooding and epinasty has also been frequently analyzed (Jackson and Campbell, 1975; Kuo and Chen, 1980; Colli, 1998). Whereas Pimenta et al. (1994) verified that application of cobalt reduced epinasty, Colli (1998) registered a slight decrease in leaf curvature by silver nitrate in flooded *Croton floribundus*.

T. avellanedae produced superficial roots in all treatments in which flooding occurred. Such a formation was not increased neither by "Ethrel" application nor inhibited by silver nitrate. This fact suggests that probably for the species under investigation ethylene may not have a direct effect in the formation of these structures. In some species the formation of new roots is principally controlled by auxins (Wample and Reid, 1979). In such cases, ethylene would have an indirect effect on roots, since it increases the sensitivity of tissues to auxins (Liu and Reid, 1992).

Responses to soil flooding are generally attributed to the effect of ethylene. Research has shown that hormone increases in hypoxia conditions (Jackson et al., 1985; Sena-Gomes and Kozlowski, 1988; Brailsford et al., 1993; Colli, 1998). Although quantities of ethylene have not been calculated, it is suggested that symptoms, such as growth decrease, may be related to ethylene. However, within the studied aspects, it is more probable that other factors besides ethylene would be working in the changes shown by species. It is thus necessary that detailed studies between different vegetal species on quantity, regulation and combined action of these substances may be undertaken so that the function of ethylene and other vegetal hormones in flooding tolerance can be understood.

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RESUMO

Plantas de *Tabebuia avellanedae* Lor. ex Griseb. (Bignoniaceae) com três meses de idade e cultivadas em casa de vegetação, foram submetidas a 56 dias alagamento e à aplicação de "Ethrel" e de nitrato de prata. Objetivou-se verificar qual a capacidade desta espécie apresentar modificações morfológicas e fisiológicas para sobreviver durante períodos de inundação e em que grau tais respostas podem estar relacionadas com alterações nos níveis de etileno. O alagamento e a aplicação de "Ethrel" provocaram redução do crescimento e epinastia em T. avellanedae e a aplicação de nitrato prata amenizou em certos aspectos estes efeitos. Alguns sintomas apresentados por esta espécie durante a inundação e sua capacidade de desenvolver estruturas que amenizam os efeitos da hipoxia, como rachaduras corticais e hipertrofia de lenticelas nas raízes (modificações que possibilitaram a adaptação a curtos períodos de inundação) podem estar relacionados a aumentos na concentração de etileno nos tecidos da planta.

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