

## BRIEF COMMUNICATION

**Embolism vulnerability of an evergreen tree**

M. A. SOBRADO

*Laboratorio de Biología Ambiental de Plantas, Departamento de Biología de Organismos, Universidad Simón Bolívar, Apartado 89.000, Caracas, Venezuela*

**Abstract**

Leaf bearing stems of *Curatella americana* L. were very susceptible to induced cavitation: embolisms began at a pressure of 0.5 MPa (15 %) and at 2.0 MPa most of the conductivity was lost (85 %). Nevertheless, in nature similar leaf specific conductivities, of about  $90 \times 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$  during both wet and dry seasons indicated absence of drought induced embolisms. Leaf water potentials were neither very negative or considerably different between seasons but stomatal conductance decreased from  $236 \text{ mmol m}^{-2} \text{ s}^{-1}$  measured during wet period to  $100 \text{ mmol m}^{-2} \text{ s}^{-1}$  during drought season. Therefore, it was concluded that *Curatella* had an accurate homeostatic balance of leaf water status to keep up xylem integrity.

*Additional key words:* *Curatella americana* L., hydraulic conductivity, stomatal conductance, water deficit, water potential.

---

*Curatella americana* L. (Dilleniaceae) is an evergreen tree scattered within neotropical savannas which maintains its canopy, leaf-exchange, flowering and carbon gain during rainless period (Blydenstein 1962, San José 1977, Goldstein *et al.* 1989, Medina and Francisco 1994). Its physiological behavior seems uncoupled from rainfall patterns prevailing in its natural habits and it has been justified that it is able to use the water from subsoil layers unavailable to grass layer (San José 1977) and it has efficient water transport system (Goldstein *et al.* 1989). Therefore, we hypothesized that under the prevailing conditions of tropical savannas the maintenance of low internal water deficit in an evergreen species with large hydraulic conductivity may be possible by reducing transpiration by stomatal control during rainless season to avoid fateful xylem failure.

---

*Received* 13 June 1995, *accepted* 12 September 1995.

*Acknowledgements:* Financial support was provided by Decanato de Investigaciones - USB (S1-CB-811). Dr John Sperry (University of Utah) allowed me to learn how to use and to build the equipment used in this study. Mr. M. Edreida and Mr. T. Pérez helped me in the field and in the laboratory, respectively. Dr D. Henríquez corrected the English grammar.

This study was conducted at Valle Morín, Estado Aragua (09° 55' 20" N, 66° 55' 10" W, 400 m) in Venezuela where average annual rainfall is 1276 mm, potential evaporation is 2037 mm and monthly mean temperature is 25.6 °C. There is a relatively dry period from December to April with only 9.01 % of rainfall and 44.77 % of potential evaporation. Plant field measurement and sampling collection was conducted in the middle of the wet (June and July 1994), and of the dry (February and March 1994) seasons. All the hydraulic parameters were measured on leaf-bearing stems using as permeating liquid a solution 1 % of HCl prepared with prefiltered (< 0.2 mm) distilled water. Large branches were cut in the field, kept in black plastic bags and brought to the laboratory where stem samples were cut under water. Stem cross-sectional areas were determined after removing the bark. Stems water contents,  $W_c$  [ $g\ g^{-1}$ (dry mass)], specific mass,  $G$ , [ $g$ (dry mass)  $cm^{-3}$ ], as well as volumetric fractions of water, solids and gas were measured on 40 to 50 samples taken from 5 different trees for each season. Water contents were estimated as the difference between fresh mass and oven-dried (80 °C) mass expressed per dry mass unit. Specific mass was obtained by expressing dry mass per fresh volume ( $V_f$ ) measured by water displacement. Water ( $V_w$ ), solids ( $V_s$ ) and gas fractions ( $V_g$ ) were estimated using the relationships outlined by Sobrado *et al.* 1992. The relationships between percentage loss of hydraulic conductance as a function of xylem tension (vulnerability curves) were evaluated by using the air-injection method (Sperry and Saliendra 1994), by measuring 5 straight stem segments averaging 20 mm<sup>2</sup> in transverse area and between 22 to 25 cm length, excised from branches cut during rainy season. Hydraulic conductance ( $K_h$ ) and percentage of native embolisms were measured by using a conductivity apparatus (Sperry *et al.* 1988). Thus,  $K_h$  from 30 to 40 segments, averaging 25 cm length and 20 mm<sup>2</sup> cross-sectional area, was assessed for wet and dry seasons. The percentage of embolism was calculated by comparing  $K_h$  values before and after embolisms removal by flushing segments under a pressure of 0.075 MPa. Leaf specific conductivities  $K_l$ , [ $kg\ m^{-2}\ s^{-1}\ MPa^{-1}$ ], defined as stem  $K_h$  expressed per unit of leaf area, were measured in 12 terminal branches per season. Huber values (HV) were calculated as the stem cross-sectional area [ $m^2$ ] per leaf area [ $m^2$ ].

Early morning and midday leaf water potential ( $\psi_w$ ) were taken in twenty healthy leaves during rainy and rainless seasons by means of a pressure chamber. Stomatal conductance and transpiration rates were measured on 60 full mature non-senescent sunny leaves during both wet and dry seasons by using a portable infra-red gas-analyzer system (*LCA-2, Analytical Development Company, Herts, England*). Irradiance for measurements was higher than 1000  $\mu mol\ m^{-2}\ s^{-1}$  and leaf temperature about 33 °C.

Embolisms began at a pressure as low as 0.5 MPa (15 %) and at 2.0 MPa 85 % of the conductivity was lost (Fig. 1). Thus, *Curatella* is comparable to the most susceptible species described for tropical environments with greater annual rainfall (Tyree *et al.* 1991, Machado and Tyree 1994).  $K_l$  estimations, which appraised the efficiency of stems to supply water to leaves, were  $92.5 \pm 12$  and  $88.78 \pm 13 \times 10^{-5}$   $kg\ m^{-2}\ s^{-1}\ MPa^{-1}$  for wet and dry season, respectively. These values were within the range of very high  $K_l$  in tropical plants from 50 to  $110 \times 10^{-5}$   $kg\ m^{-2}\ s^{-1}\ MPa^{-1}$  given

for Machado and Tyree (1994). Huber values (HV) did not change between seasons and averaged  $1.55 \pm 0.19 \times 10^{-4}$  for stem segments with a cross-sectional area of  $35.4 \pm 0.4 \text{ mm}^2$ . Thus, large  $K_1$  in *Curatella* was related to its large investment in cross-sectional area stems per unit leaf area. Percentage of embolisms were  $29.52 \pm 6.75 \%$  (wet season) and  $33.84 \pm 5.02 \%$  (dry season) and the difference between seasons was not statistically significant. Thus,  $K_1$  and occurrence of embolisms gave compelling evidence of lack of drought-induced xylem dysfunction in *Curatella*. Given the large  $K_1$  observed in *Curatella* over seasons, slight diurnal variations of stem  $\psi_w$  would be expected. However, midday leaf  $\psi_w$  (Table 1) may not be an accurate appraisal of stem  $\psi_w$  (Borchert 1994). This is because leaf blades resistance of non-vascular path account for about 50 % of the whole-shoot resistance (Yang and Tyree 1994), and it may be responsible for low leaf  $\psi_w$  measured with a pressure chamber. Nevertheless, early morning leaf  $\psi_w$  may be a better indication of stem  $\psi_w$ , and the values of *Curatella* were similar between seasons (Table 1). Within this water potential range, conductivity loss was very small (Fig. 1). Nevertheless,

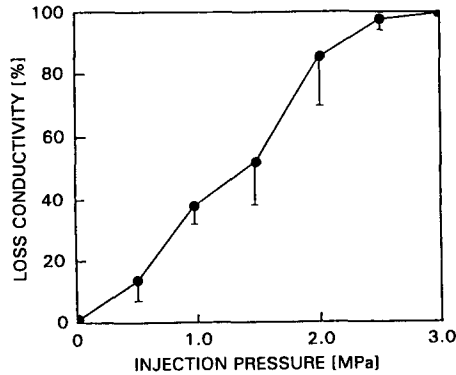


Fig. 1. Percentage of conductivity loss as a function of injection pressure in *Curatella americana* during wet season (means of 5 observations, bars represent standard deviations).

Table 1. Water content ( $W_c$ ), specific gravity ( $G$ ), volumetric fraction of water ( $V_w$ ), of solids ( $V_s$ ) and gas ( $V_g$ ) of wood, and maximum and minimum water potentials ( $\psi_w$ ), stomatal conductance ( $g_s$ ) and transpiration rate ( $E$ ) of leaves, measured during both wet and dry seasons in *Curatella americana*.

Wood			Leaf		
	wet	dry		wet	dry
$W_c$ [ $\text{g g}^{-1}$ ]	$1.85 \pm 0.21$	$1.39 \pm 0.19$	$\psi_{w \text{ max}}$ [MPa]	$-0.4 \pm 0.1$	$-0.5 \pm 0.1$
$G$ [ $\text{g cm}^{-3}$ ]	$0.37 \pm 0.03$	$0.41 \pm 0.04$	$\psi_{w \text{ min}}$ [MPa]	$-1.2 \pm 0.1$	$-1.5 \pm 0.1$
$V_w$	$0.64 \pm 0.03$	$0.57 \pm 0.04$	$g_s$ [ $\text{mmol m}^{-2}\text{s}^{-1}$ ]	$236.0 \pm 75.0$	$100.0 \pm 39.0$
$V_s$	$0.23 \pm 0.02$	$0.27 \pm 0.02$	$E$ [ $\text{mmol m}^{-2}\text{s}^{-1}$ ]	$6.9 \pm 0.3$	$4.2 \pm 0.2$
$V_g$	$0.13 \pm 0.03$	$0.16 \pm 0.03$			

regulation of stomatal aperture and water loss were observed during rainless season (Table 1). Coordination of both, water loss and transport capacity aid the preservation of constant leaf water status and of xylem integrity (Tyree and Sperry 1988, 1989, Meinzer and Grantz 1990). Stomatal regulation may also be important to improve water use efficiency and conserve water for later use as predicted by optimal stomatal behavior (Jones and Sutherland 1991). In this case, it could not be discarded that the drying soil  $\psi_w$  may be the signal inducing stomatal regulation in *Curatella*, instead of changes in leaf  $\psi_w$  as it has been found in other studies (Gollan *et al.* 1985).

Changes in stem water content ( $W_c$ ) as well as in wood volumetric fractions of water ( $V_w$ ), solids ( $V_s$ ) and gas ( $V_g$ ) were obtained during rainless period and concomitantly with this, specific gravity (G) increased only moderately (Table 1). *Curatella* could be considered a tropical light-wood tree ( $G < 0.5 \text{ g cm}^{-3}$  and  $W_c > 1.25 \text{ g g}^{-1}$  (dry mass); Schulze *et al.* 1988, Borchert 1994 a,b). Minor variation of  $V_s$  from wet to dry season is consistent with the small increase of G during the dry season. By contrast, the largest and most significant decline throughout drought was suffered by  $V_w$  which is consistent with diminished  $W_c$ . It is conceivable that water stores may be released diurnally to aid the prevention embolisms in *Curatella* with stems highly vulnerable to embolize. This is a well recognized mechanism to amend water supply by roots at periods of high evaporative demand or soil water shortage to prevent low  $\psi_w$  and xylem failure (Waring *et al.* 1979, Tyree and Yang 1990, Hollbrook and Sinclair 1992).

In conclusion the leaf-bearing stems of *Curatella americana* L. were highly vulnerable to suffer cavitation but its specific leaf conductivities were maintained unchanged throughout the seasons suggesting the occurrence of very few embolisms. Lowered transpiration rates ameliorated water demand on a diurnal basis during rainless season. It was proposed that *Curatella* had an accurate homeostatic balance of leaf water status and control to keep up xylem integrity.

## References

- Blydenstein, J.: [The *Trachypogon* savannas]. - Bol. Soc. Ven. Cienc. Nat. 23: 139-238, 1962. [In Span.]
- Borchert, R.: Soil and stem water storage determine phenology and distribution of tropical dry forest trees. - Ecology 75: 1437-1449, 1994a.
- Borchert, R.: Water status and development of tropical trees during seasonal drought. - Trees 8: 115-125, 1994b.
- Jones, H.G., Sutherland, R.A.: Stomatal control of xylem embolisms. - Plant Cell Environ. 14: 607-612, 1991.
- Goldstein, G., Rada, F., Rundel, P., Azócar, A., Orozco, A.: Gas exchange and water relations of evergreen and deciduous tropical savannas trees. - Ann. Sci. forest. 46: 448-453, 1989.
- Gollan, T., Passioura, J.B., Munns, R.: Soil water status affects the stomatal conductance of fully turgid wheat and sunflower leaves. - Aust. J. Plant Physiol. 13: 459-464, 1985.
- Holbrook, N.M., Sinclair, T.R.: Water balance in the arborescent palm, *Sabal palmeto*. II. Transpiration and stem water storage. - Plant Cell Environ. 15: 401-409, 1992.

- Machado, J.L., Tyree, M.T.: Patterns of hydraulic architecture and water relations of two tropical canopy trees with contrasting leaf phenologies: *Ochroma pyramidale* and *Pseudobombax septenatum*. - *Tree Physiol.* **14**: 219-240, 1994.
- Meinzer, F.C., Grantz, D.A.: Stomatal and hydraulic conductance in growing sugarcane: Stomatal adjustment to water transport capacity. - *Plant Cell Environ.* **13**: 383-388, 1990.
- Medina, E., Francisco, M.: Photosynthesis and water relations of savanna tree species differing in leaf phenology. - *Tree Physiol.* **14**: 1367-1381, 1994.
- San José, J.J.: [Water potential and leaf gas exchange of *Curatella americana* L. during rainless period in *Trachypogon* savannas.] - *Acta Cient. Ven.* **28**: 373-379, 1977. [In Span.]
- Schulze, E.-D., Mooney, H.A., Bullock, S.H., Mendoza, A.: Water contents of a tropical deciduous forest species during the dry season. - *Bol. Soc. Bot. México* **48**: 113-118, 1988.
- Sobrado, M.A., Grace, J., Jarvis, P.G.: The limits to xylem embolism recovery in *Pinus sylvestris* L. - *J. exp. Bot.* **43**: 831-836, 1992.
- Sperry, J.S., Donnelly, R.R., Tyree, M.T.: A method for measuring hydraulic conductivity and embolism in xylem. - *Plant Cell Environ.* **11**: 35-40, 1988.
- Sperry, J.S., Saliendra N.Z.: Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. - *Plant Cell Environ.* **17**: 1233-1241, 1994.
- Tyree, M.T., Snyderman, D.A., Wilmont, T.R., Machado, J.L.: Water relations and hydraulic architecture of a tropical tree (*Schefflera morotoni*). Data, models, and a comparison with two temperate species (*Acer saccharum* and *Thuja occidentalis*). - *Plant Physiol.* **96**: 1105-1113, 1991.
- Tyree, M.T., Sperry, J.S.: Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. - *Plant Physiol.* **88**: 574-580, 1988.
- Tyree, M.T., Sperry, J.S.: Vulnerability of xylem to cavitation and embolisms. - *Annu. Rev. Plant Physiol. Plant mol. Biol.* **40**: 19-38, 1989.
- Waring, R.H., Whitehead, D., Jarvis, P.G.: The contribution of stored water to transpiration in Scots pine. - *Plant Cell Environ.* **2**: 309-317, 1979.
- Yang, S., Tyree, M.T.: Hydraulic architecture of *Acer saccharum* and *A. rubrum*: Comparison of branches to whole trees and the contribution of leaves to hydraulic resistance. - *J. exp. Bot.* **45**: 179-186, 1994.