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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 × 10^{-5} kg m^{-2} s^{-1} 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 mmol m^{-2} s^{-1} measured during wet period to 100 mmol m^{-2} 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.

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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^2 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^2 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 (ψ_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 μmol 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 ± 12 and 88.78 ± 13 × 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 × 10^{-5} kg m^{-2} s^{-1} MPa^{-1} given for Machado and Tyree (1994). Huber values (HV) did not changed between seasons and averaged 1.55 ± 0.19 × 10^{-4} for stem segments with a cross-sectional area of 35.4 ± 0.4 mm^2. Thus, large K_l in *Curatella* was related to its large investment in cross-sectional area stems per unit leaf area. Percentage of embolisms were 29.52 ± 6.75 % (wet season) and 33.84 ± 5.02 % (dry season) and the difference between seasons was not statistically significant. Thus, K_l and occurrence of embolisms gave compelling evidence of lack of drought-induced xylem disfunction in *Curatella*. Given the large K_l observed in *Curatella* over seasons, slight diurnal variations of stem ψ_w would be expected. However, midday leaf ψ_w (Table 1) may not be an accurate appraisal of stem ψ_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 ψ_w measured with a pressure chamber. Nevertheless, early morning leaf ψ_w may be a better indication of stem ψ_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,

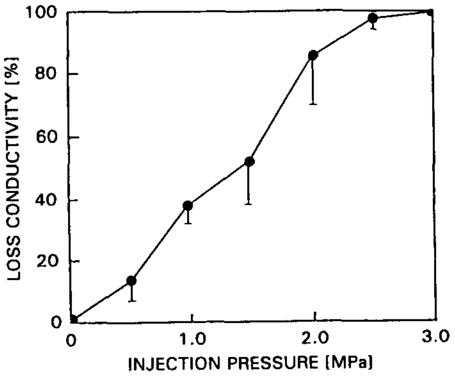

Fig. 1. Percentage of conductivity loss as a function of injection pressure in *Curatella americana* during wet season (means of 5 observations, *bars* represent standard deviations).

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 (ψ_w), stomatal conductance (g_s) and transpiration rate (E) of leaves, measured during both wet and dry seasons in *Curatella americana*.

Wood	wet	dry	Leaf	wet	dry
W_c [g g^{-1}]	1.85 ± 0.21	1.39 ± 0.19	$\psi_{w\,max}$ [MPa]	-0.4 ± 0.1	-0.5 ± 0.1
G [g cm^{-3}]	0.37 ± 0.03	0.41 ± 0.04	$\psi_{w\,min}$ [MPa]	-1.2 ± 0.1	-1.5 ± 0.1
V_w	0.64 ± 0.03	0.57 ± 0.04	g_s [mmol $m^{-2}s^{-1}$]	236.0 ± 75.0	100.0 ± 39.0
V_s	0.23 ± 0.02	0.27 ± 0.02	E [mmol $m^{-2}s^{-1}$]	6.9 ± 0.3	4.2 ± 0.2
V_g	0.13 ± 0.03	0.16 ± 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 been discarded that the drying soil ψ_w may be the signal inducing stomatal regulation in *Curatella*, instead of changes in leaf ψ_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 ($G < 0.5$ g cm^{-3} and $W_c >$ 1.25 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 ψ_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.

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