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BRIEF COMMUNICATION

Hydraulic conductance and water potential differences inside leaves of tropical evergreen and deciduous species

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Abstract

Several pieces of research suggest that leaf liquid-path conductance (K_l) may be smaller in evergreen species (EG) than in deciduous species (DC), coexisting in tropical dry forests. This was investigated in four DC and two EG in a tropical dry forest in Venezuela. The K_l (kg m^{-2} MPa^{-1} s^{-1}) were consistently lower in EG (8.4×10^{-5}) than in DC (12 to 20×10^{-5}). Differences in water potential ($\Delta\Psi_w$) inside the leaves were calculated using K_l values in connection with maximum transpiration rates measured in the field. It was found that $\Delta\Psi_w$ was about 1.9 MPa in EG, intermediate for one DC (*Pithecellobium dulce*, 1.7 MPa) and minimum for other DC (1.0 to 1.3 MPa).

Additional key words: *Beureria cumanensis*, *Capparis aristiguetae*, *Coursetia arborea*, *Lonchocarpus dipteroneurus*, *Morisonia americana*, *Pithecellobium dulce*.

In tropical dry forests, midday leaf water potentials (Ψ_w) of sclerophyllous evergreen species (EG) are low during both rainy and dry season (Sobrado and Cuenca 1979, Borchert 1994). Nonetheless, to avoid severe embolization of leaf bearing shoots, such low Ψ_w seem to be restricted to leaves and excluded from stems (Sobrado 1997). Moreover, a drop in Ψ_w from the base of the petiole to the evaporative surface

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Abbreviations: A - leaf area; DC - deciduous species; E - transpiration rate; EG - evergreen species; F - water flow; HPFM - high pressure flowmeter, K_l - leaf liquid-path conductance, K_s - shoot conductance; P - pressure; R_l - leaf resistance; Ψ_w - leaf water potential; $\Delta\Psi_w$ - water potential drop from petiole to evaporative surface.

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of the lamina ($\Delta\Psi_w$) has been shown to be relatively large in a number of species (Tyree *et al.* 1993). Thus, I hypothesized that EG may have lower leaf liquid-path conductance than coexisting drought-deciduous species (DC), and that may lead to larger $\Delta\Psi_w$ in their leaves in comparison to DC. Rapid determination of conductance of liquid flow in leaves is now possible after the introduction of a high pressure flowmeter (HPFM; Tyree *et al.* 1995). Therefore, leaf liquid-path conductance and maximum transpiration rate were determined in 4 deciduous and 2 evergreen species coexisting in a tropical dry forest in Venezuela.

The experimental site was a tropical dry forest located in Venezuela at 10 °N, 67 °W, and 400 m elevation. Annual rainfall is 900 mm with a marked dry season between December and May. The species used in this study were 4 deciduous [*Coursetia arborea* (=*Humboldtiella arborea* Griseb), *Lonchocarpus dipteroneurus* Pittier, *Pithecellobium dulce* Benth and *Beureria cumanensis* Schulz] and 2 evergreens (*Morisonia americana* L. and *Capparis aristiguetae* Iltis) (for more details see Sobrado 1986, 1991, 1997).

Shoots bearing new fully expanded sun leaves were collected in the field during the wet season, when water stress was minimal. They were stored in plastic bags with a small amount of water added to avoid dehydration. The material was transported back to the laboratory and measured the same day of collection. Measurements were conducted in 11 to 17 shoots per species, of 3 to 5 mm diameter and with a total leaf area (A) of 0.05 to 0.30 m^2. Shoot conductance (K_S), before and after leaf removal, was measured with a high-pressure flowmeter (HPFM), available commercially (*Dynamax Inc.* Houston, Texas, USA), similarly as described Tyree *et al.* (1995). This instrument allows rapid measurements of water flow (F, [kg s^{-1}]) while controlling the pressure (ΔP, MPa). The base of each shoot was connected to the

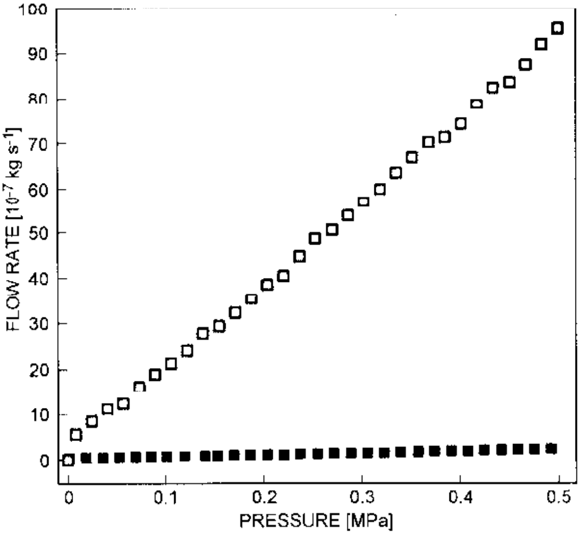

Fig. 1. Typical transient measurement of flow rate (F) as a function of applied pressure (P), on a *Capparis aristiguetae* shoot with leaves (*closed squares*) and without leaves (*open squares*).

HPFM, and perfused at a pressure of 0.4 MPa for 20 min. This was done in order to infiltrate the leaves, to ensure that their water potential was equal to zero. Subsequently, F was measured at 4 s intervals, while P was changed at a constant rate of 3 to 5 kPa s^{-1} (Fig. 1). Leaves were removed from shoots and the outlined routine repeated. Shoot conductance was computed as the slope of the relationship of F *vs* P over the range of pressure recorded measurements (transient measurements, Tyree *et al.* 1995). From these results the resistance of leaves (R_l) was calculated by subtracting the resistance of the shoots without leaves from the resistance of shoots with leaves. Leaf conductance per unit leaf area (K_l) was calculated as the inverse of R_l multiplied by leaf area ($K_l = 1/R_lA$). Transpiration rates (E) were measured in the field during the wet season, with a portable gas exchange system (*LCA-2*, *ADC*. Herts, England). The measurement was taken for 20 to 30 leaves exposed to the sun at a leaf temperature of about 30 °C, irradiance of 1 000 μmol m^{-2} s^{-1} and an ambient CO_2 pressure of about 34 Pa. $\Delta\Psi_w$ was calculated for each species by using the means of E and K_l ($\Delta\Psi_w = E/K_l$).

In all species shoot conductance (K_s) measured with leaves attached were lower than K_s with detached leaves (Table 1). However, in DC, values of K_s only increased 2 to 4 times after leaves were detached. Conversely, very large increases in K_s were observed in EG shoots after leaves detached (13 to 22 times). This suggests that the leaf resistance may represent the biggest liquid-path resistance within EG plants. Conversely, in DC, except in *P. dulce*, leaf resistances to water flow seem to be more closely coupled to those in stems. Leaf conductance (K_l) for DC ranged from 12 to 20 × 10^{-5} and from 8.4 to 9.0 × 10^{-5} kg m^{-2} MPa^{-1} s^{-1} in EG. The low K_l would be potentially limiting for the EG, if an excessive gradient in Ψ_w developed within the leaf, leading to decreased gas exchange. In fact, $\Delta\Psi_w$ in the leaf increased considerably when K_l decreased (Table 2). Thus on average the drops in $\Delta\Psi_w$ were about 1.9 MPa in EG, intermediate for one DC (*P. dulce*, 1.7 MPa) and minimum for other DC (1.0 × 10^{-5} to 1.3 × 10^{-5} MPa). Transpiration rates were not very different between DC (11 × 10^{-5} to 16 × 10^{-5} kg m^{-2} s^{-1}) and EG (14 × 10^{-5} kg m^{-2} s^{-1}).

Table 1. Hydraulic conductances (K_s) measured on shoots with leaves and without leaves of drought-deciduous and evergreen species. Values are means ± S.D., *n* = 11 - 17. Least significant difference (LSD) at $P < 0.05$ are indicated for each parameter.

Species		K_s [10^{-6} kg Mpa^{-1} s^{-1}] with leaves	without leaves
Drought-decidious	*C. arborea*	3.25 ± 0.98	9.92 ± 1.67
	L.dipteroneurus	2.07 ± 0.92	6.02 ± 1.34
	B. cumanensis	1.05 ± 0.12	4.33 ± 1.30
	P. dulce	1.71 ± 0.50	4.19 ± 1.37
Evergreen	*M. americana*	2.29 ± 0.31	28.75 ± 4.79
	C. aristiguetae	1.51 ± 0.19	33.33 ± 4.33
	LSD	1.85	5.90

Despite the fact that stems of EG are similarly susceptible to those of DC in suffering runaway embolisms (Sobrado 1997), their leaves are better adapted to undergo very large $\Delta\Psi_w$ before turgor is zero (Sobrado 1986). Therefore, low Ψ_w in EG is confined to leaves but not to stems. Although the occurrence of embolisms has been related to leaf Ψ_w, it has been recognized that stem Ψ_w are somewhat higher (Jones and Sutherland 1991). Moreover, in tropical dry forests, the difference between stem and leaf Ψ_w in DC is very small, but can be up 3 MPa in EG (Borchert 1994). K_l could be particularly limiting under water supply restrictions and large water loss. In that case, K_l may limit stomatal conductance through its effects on the Ψ_w of guard cells (Tyree *et al.* 1998). Severe restriction in E has been observed in DC at the onset of drought and in EG by the end of dry season (Sobrado and Cuenca 1979). The fact that HPFM may overestimate the true conductance of the transpiration stream (Tyree *et al.* 1998) mean that calculated gradients may be in consequence underestimated. Moreover, given that measurements were conducted on perfused material collected during the wet season, it is probable that true conductance is much lower during the dry season particularly in drought sensitive DC.

Table 2. Leaf liquid-path conductance, K_l, and $\Delta\Psi_w$ of drought-deciduous and evergreen species. Values are means ± S.D., $n = 11 - 17$. Least significant difference (LSD) at $P < 0.05$ are indicated for each parameter.

Species		K_l [$\times 10^{-5}$ kg m^{-2} Mpa s^{-1}]	$\Delta\Psi_w$ [MPa]
Drought-deciduous	*C. arborea*	12.43 ± 1.24	1.20 ± 0.15
	L. dipteroneurus	14.24 ± 3.24	1.29 ± 0.21
	B. cumanensis	19.63 ± 2.18	0.98 ± 0.10
	P. dulce	12.50 ± 2.24	1.66 ± 0.30
Evergreen	*M. americana*	8.97 ± 0.98	1.86 ± 0.17
	C. aristiguetae	8.38 ± 0.69	1.83 ± 0.14
	LSD	2.81	0.46

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