

Embolism vulnerability in drought-deciduous and evergreen species of a tropical dry forest

M. A. Sobrado

Laboratorio de Biología Ambiental de Plantas. Depto. Biología de Organismos.
Universidad Simón Bolívar. Aptdo. 89.000. Caracas 1080 A, Venezuela.
e-mail:msobrado@skynet.usb.ve

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Abstract

Plant water status plays an important role in determining phenological patterns of leaf expansion and abscission of drought-deciduous (DC) and evergreen (EG) species co-occurring in tropical dry forests. If vulnerability to embolism is related to the phenological pattern, we should find that drought-deciduous species are intrinsically more susceptible than evergreen species to drought-induced embolisms. The object of this study was to assess the embolism vulnerability curves and the percentage loss of hydraulic conductivity (PLC) due to embolisms in four DC and two EG species from a tropical dry forest in Venezuela. In DC, PLC was between 8 and 19% during the wet season but a significant increase to between 38 and 79% occurred during the dry season. Increment of embolism in EG was from 30 to 35% during the wet season to between 40 and 48% during the dry season. Regarding embolism vulnerability curves, a clear-cut difference between DC and EG species was not observed. Both plant types underwent 50 PLC at a cavitation tension between 1.65 and 3.82 MPa. In conclusion, the degree of embolism in DC and EG was not determined by differences in vulnerability curves. Moreover, no interrelation was found between xylem efficiency and tension at 50 PLC embolisms. Differences in root depth and water availability between DC and EG seemed to be the underlying cause of embolism in the field. Nevertheless, the occurrence of a lower susceptibility to drought-induced embolisms in the dominant tree *B. cumanaensis* implied that risk from xylem dysfunction may have some ecological significance.

Keywords: Cavitation, deciduous trees, embolism vulnerability, hydraulic conductance, sclerophylls evergreen, tropical forest, water relations, xylem dysfunction.

Résumé

L'état hydrique des plantes joue un rôle important dans le déterminisme phénologique du développement et de l'abscission foliaires d'espèces décidues (effet sécheresse) et sempervirentes poussant dans les mêmes forêts tropicales sèches. Si la vulnérabilité à l'embolie est liée au patron phénologique, nous devrions trouver que les espèces décidues sont intrinsèquement plus sensibles que les espèces sempervirentes aux embolies provoquées par la sécheresse. L'objet de cette étude est de déterminer des courbes de vulnérabilité à l'embolie ainsi que le pourcentage de perte de conductivité hydraulique (PLC) due à l'embolie chez quatre espèces décidues et deux espèces sempervirentes d'une forêt tropicale sèche du Vénézuéla. Chez les espèces décidues, la PLC se situe entre 8 et 19% au cours de la saison humide, mais présente une augmentation significative

(de 38 à 79%) au cours de la saison sèche. Chez les espèces sempervirentes, l'embolie passe de 30 à 35% en saison humide à 40 à 48 % en saison sèche. En ce qui concerne les courbes de vulnérabilité à l'embolie, nous n'avons pas observé de différence marquée entre les espèces décidues et sempervirentes. Les deux types de plantes subissent une PLC de 50 pour une tension de cavitation de 1.65 à 3.82 MPa. En conclusion, le degré d'embolie chez les deux types d'espèces ne peut pas être déterminé par des différences dans les courbes de vulnérabilité. De plus, aucune relation n'a été trouvée entre l'efficacité du xylem et la tension pour des embolies de 50 PLC. Des différences dans la profondeur des racines et la disponibilité en eau entre les deux types d'espèces semblent être la cause sous-jacente aux embolies sur le terrain. Cependant, la plus faible sensibilité de l'arbre dominant *B. cumanensis* à l'embolie due à la sécheresse implique que le risque lié à un dysfonctionnement du xylem peut avoir une signification écologique.

INTRODUCTION

Gradients of xylem tension arise in transpiring plants with the lowest tension located in the roots and the highest in the transpiring leaf. Xylem embolism occurs if xylem tension is sufficiently large to cause air seeding, *i.e.* aspiration of a vessel via pores in the wall adjacent to an air space (OERTLI, 1971; ZIMMERMANN, 1983; SPERRY & TYREE, 1988; SPERRY *et al.*, 1991; COCHARD *et al.*, 1992; JARBEU *et al.*, 1995). Thus, air seeding is especially likely during drought, as high xylem tension occurs when the soil dries. Water transport stops in the air-seeded vessel because of the resulting cavitation of water and the replacement of water with gas (SPERRY & TYREE, 1988). Therefore, drought predisposes plants to xylem embolism and consequently a significant proportion of the xylem may be unavailable for water flow. The vulnerability of xylem to embolism determines the dynamics of loss of hydraulic conductivity in stems as the water potential declines. The decline in water potential is related to water acquisition by roots, and to water loss from the leaves.

Tropical dry forests are dominated by species that remain leafless during the dry season, often they coexist with a few evergreen species. It has been recognized that plant water status plays an important role in determining seasonal patterns in leaf expansion and abscission of both drought-deciduous and evergreen species co-occurring in tropical dry forests (REICH & BORCHERT, 1982; TUGUES, 1982; BULLOCK & SOLÍS-MAGALLANES, 1990). Both plant types have a combination of morphological (SOBRADO & CUENCA, 1979) and physiological (SOBRADO, 1986, 1991, 1995; SCHULZE *et al.*, 1988; GARTNER *et al.*, 1990; OLIVARES & MEDINA, 1992; BORCHERT, 1994 *a, b*) properties that adapts them to periods of low water availability. Hydraulic conductivity is higher in drought-deciduous than in evergreen woody species, but conductivity is severely reduced in times of drought in these species due to the occurrence of embolisms (SOBRADO, 1993). The behaviour of evergreen species in contrast is conservative, maintaining constant conductivity during wet and dry seasons indicating that fewer embolisms occur. It may be possible that vulnerability to embolism is the ultimate cause of dissimilar phenological patterns in deciduous and evergreen species. The object of this study was to assess the embolism vulnerability curves in four drought-deciduous and two evergreen species from a tropical dry forest in Venezuela. The comparison is discussed in relation to the degree of embolism naturally occurring during rainy and dry seasons. If vulnerability to embolism is related to the phenological pattern, we should find that drought-deciduous species are intrinsically more susceptible than evergreen species to drought-induced xylem embolisms.

PLANT MATERIAL AND METHODS

Field site and species

Plant material was collected in a forest at Charallave (Estado Miranda, Venezuela) located at an elevation of 400 m and 10°15'N 67°03'W. Annual mean temperature is 24.6 °C and mean precipitation 900 mm. Most of the annual rainfall occurs during the rainy season between May and October (700 mm). The plant species used were four drought-deciduous (DC) trees: *Coursetia arborea* (= *Humboldtiella arborea* Griseb): Leguminosae; *Lonchocarpus dipteroneurus* Pittier: Leguminosae; *Beureria cumanensis* Schulz: Boraginaceae and *Pithecellobium dulce* Benth: Leguminosae and two evergreen (EG) species: the shrub *Capparis aristiguetae* Itis Capparidaceae; and the tree *Morisonia americana* L: Capparidaceae. They are representative of the phytosociologically dominant DC and more common EG species. Field site, climate and plant species have been described in more detail elsewhere (SOBRADO & CUENCA, 1979; SOBRADO, 1991, 1993).

Hydraulic measurements

All the hydraulic assessments were made on terminal branches of the upper crown as these are considered more at risk from xylem dysfunctions (ZIMMERMANN, 1983). Branches were bagged and wetted in the field and they were cut and maintained under water in the laboratory. All the measurements were completed within 5 to 8 h of collection. In order to prevent microbial growth, the permeating liquid was a solution of HCl (pH 2) in prefiltered water (0.2 μm) as recommended by SPERRY & SALIENDRA (1994). Hydraulic conductivity of the stem segments (K_h , $\text{kg m}^{-1} \text{MPa}^{-1}$) was defined as the mass of water that passes per unit of time (kg s^{-1}) divided by the gradient pressure (MPa m^{-1}). Expressing K_h per distal leaf area and per stem transverse area gave leaf specific conductivity (K_l , $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) and specific conductivity (K_s , $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$), respectively. The length, diameter and leaf area for each stem-sample were recorded, as required for further calculations. Huber values (HV, m m^{-2}) were calculated as the stem cross-sectional area (m^2) per leaf area (m^2).

Leaf specific conductivity

Plant material was collected when the water content of the woody tissues was maximal during the rainy season (June and July) and minimal during the dry season (January and February; SOBRADO, 1993). K_l was measured in 12 branches per species taken only when the plants had leaves (wet season) for DC and during both wet and dry season for EG. The relationship between water weight that passes along the stem-segment per unit of time (kg s^{-1}) as a function of three gradient pressures (0.08, 0.17 and 0.25 MPa m^{-1}) was determined for each sample with the leaves removed. The slope of this linear relationship was K_h for the sample, which was divided by terminal leaf area to obtain K_l and by stem transverse area to obtain K_s .

Percentage loss of hydraulic conductivity (PLC) due to embolisms

PLC values were calculated in at least 30 terminal stem segments per species per season. Stem segments were cut under water and the percentage in K_h reduction was measured by comparing the hydraulic conductivity before and after perfusion at high-pressure (100 kPa) to remove air embolism (SPERRY *et al.*, 1987). Two to three perfusions of ten minutes each were enough to reach constant conductivity of the segments.

Vulnerability curves

Curves of vulnerability to water-stress-induced embolism were determined from the interdependence between stem water potential (air-injection method) and percentage loss of hydraulic conductivity of stem-segments. These curves were obtained from six stem segments per species, clipped from branches collected in the field during the rainy season. The stem segments of 22 cm length and 5-7 mm diameter were cut under water from just below leaf-bearing stems. We used the method of air-injection pressure (0.1 to 6.0 MPa) in a double-ended pressure chamber with both ends protruding as described by SPERRY & SALIENDRA (1994). Briefly, the method consists of assessing the reduction of K_h , as a percentage of initial measurement, when the effective stem water potential is lowered in steps by forcing air into the vascular system from outside. We subjected the stem segments to 10 minutes of air-injection pressure, then the pressure was relieved and K_h measurements were carried out at a pressure difference of 0.1 MPa. This procedure was repeated for each pressure until the K_h values were stable.

RESULTS

The higher leaf specific conductivity (K_l) of drought-deciduous species (DC) in relation to evergreen species (EG) was due to greater intrinsic hydraulic conductivity (K_h) per stem transverse area (K_s ; Table I). However, Huber values (HV) were lower in DC than in EG (Table I).

Percentage loss of hydraulic conductivity (PLC) of DC and EG during wet and dry seasons demonstrated a substantial difference between both plant types (Table II). In DC, PLC was between 8 to 19% during the wet season but a significant increase to 38 to 79% occurred during the dry season. PLC in EG was from 30 to 35% during the wet season to 40 to 48% during the dry season, but these differences were not significant. The decline of K_h during the wet season,

TABLE I. – Branch transverse area, leaf area, Huber value (HV) and hydraulic conductivity (K_h) from samples used for determinations of leaf specific conductivity (K_l) and specific conductivity (K_s). Measurements were conducted during wet season in drought-deciduous species and for both wet and dry season in evergreen species. Each value is the mean \pm standard error of 12 measurements per species per season. Means followed by the same letter were not statistically different at $p < 0.05$.

| Species | Branch characteristics | | | Hydraulic characteristics | | |
|-------------------------|------------------------------------|-----------------------------|---|--|--|---|
| | Transverse area (mm ²) | Leaf area (m ²) | HV $\times 10^{-4}$ (m ² m ⁻²) | $K_h \times 10^{-6}$ (Kg m s ⁻¹ MPa ⁻¹) | $K_l \times 10^{-5}$ (Kg s ⁻¹ m ⁻¹ MPa ⁻¹) | K_s (Kg s ⁻¹ m ⁻¹ MPa ⁻¹) |
| Deciduous | | | | | | |
| <i>C. arborea</i> | 6.86 \pm 0.65a | 0.09 \pm 0.01a | 0.81 \pm 0.09a | 8.57 \pm 2.21b | 9.19 \pm 2.87a | 1.26 \pm 0.38a |
| <i>L. dipteroneurus</i> | 11.43 \pm 0.88bc | 0.12 \pm 0.02b | 0.88 \pm 0.14a | 11.01 \pm 1.43a | 9.63 \pm 0.97a | 0.98 \pm 0.13a |
| <i>P. dulce</i> | 9.78 \pm 0.79b | 0.07 \pm 0.01c | 1.53 \pm 0.16b | 5.13 \pm 0.86bcd | 7.06 \pm 1.04a | 0.54 \pm 0.09b |
| <i>B. cumanensis</i> | 14.69 \pm 1.18c | 0.06 \pm 0.01c | 2.94 \pm 0.32e | 6.03 \pm 1.20bc | 9.95 \pm 1.33a | 0.41 \pm 0.07b |
| Evergreen | | | | | | |
| <i>C. aristiguetae</i> | | | | | | |
| Wet season | 25.81 \pm 3.32de | 0.13 \pm 0.02b | 2.10 \pm 0.26bcd | 2.31 \pm 0.58e | 1.58 \pm 0.23c | 0.09 \pm 0.02c |
| Dry season | 21.11 \pm 1.73d | 0.10 \pm 0.01a | 2.20 \pm 0.20cde | 2.42 \pm 0.32de | 2.43 \pm 0.17b | 0.12 \pm 0.02c |
| <i>M. americana</i> | | | | | | |
| Wet season | 29.50 \pm 3.04e | 0.11 \pm 0.01b | 2.76 \pm 0.29de | 4.11 \pm 0.70bcd | 3.47 \pm 0.56b | 0.14 \pm 0.02c |
| Dry season | 25.43 \pm 1.46de | 0.13 \pm 0.03b | 2.18 \pm 0.43cde | 3.21 \pm 1.08cde | 3.21 \pm 0.48b | 0.14 \pm 0.05c |

TABLE II. – Branch length and transverse area, and percent loss of hydraulic conductivity (PLC) due to embolisms of terminal branches measured in drought-deciduous and evergreen species during both wet and dry seasons. Differences in PLC (Δ PLC) between wet and dry season are indicated. Each value is the mean \pm standard error per species per season. Means followed by the same letter were not statistically different at $p < 0.05$.

| Species | Branch characteristics | | PLC | | Δ PCL |
|-------------------------|------------------------|---------------------------------------|----------------------|-------------------|-----------------|
| | Length (m) | Transverse area (mm ²) | Wet | Dry | |
| Deciduous | | | | | |
| <i>C. arborea</i> | 0.21 \pm 0.01 ab | 8.17 \pm 0.94a | 17.72 \pm 4.23 ** | 38.07 \pm 0.40 | 20.35 |
| <i>L. dipteroneurus</i> | 0.20 \pm 0.01 a | 7.74 \pm 0.56a | 19.37 \pm 2.84 *** | 67.77 \pm 4.88 | 48.40 |
| <i>P. dulce</i> | 0.22 \pm 0.01 b | 7.41 \pm 0.84a | 16.01 \pm 7.15 *** | 78.72 \pm 6.63 | 62.71 |
| <i>B. cumanensis</i> | 0.20 \pm 0.01 a | 9.62 \pm 0.46b | 8.57 \pm 2.12 *** | 47.91 \pm 5.12 | 39.24 |
| Evergreen | | | | | |
| <i>C. aristiguetae</i> | 0.21 \pm 0.01 ab | 33.96 \pm 2.78d | 30.58 \pm 4.73 NS | 40.77 \pm 12.45 | 10.19 |
| <i>M. americana</i> | 0.21 \pm 0.01 ab | 23.34 \pm 1.62c | 34.59 \pm 5.33 NS | 48.24 \pm 20.33 | 13.63 |

particularly in EG, means that some embolisms may have been carried out over the previous dry season or may be the result of refilling old non-functional xylem.

Turning to the relationships between conductivity loss as a function of stem water potential (vulnerability curves), little difference between DC and EG species was observed (Fig. 1). Both plant types underwent 50 PLC at a cavitation tension between 1.65 to 2.42 MPa, except *B. cumanensis* which did not achieve a 50 PLC until 3.82 MPa.

DISCUSSION

Larger K_t found in DC compared to EG species represents considerable investment in vascular structure that allows the supply of sufficient water to leaves when water is available. In tropical dry forests, usually, DC (39 to 208 vessels/mm²) have more vessels than EG (42 to 87 vessels/mm²; LINDORF, 1994). In general, K_t values in this study were smaller than in other tropical trees from areas where the annual rainfall is higher (GOLDSTEIN *et al.*, 1989; TYREE *et al.*, 1991; MACHADO & TYREE, 1994; KOTZ *et al.*, 1994; PATIÑO *et al.*, 1995; SOBRADO, 1996). Moreover, the findings in this study are contrary to previous research on tropical savanna where EG have larger K_t than DC (GOLDSTEIN *et al.*, 1989; SOBRADO, 1996). Except in *B. cumanensis*, terminal leaf area supported by DC was greater than that of EG per stem transverse area. Thus, HV was lower in DC than in EG. The HV is more directly related to mechanical properties than to hydraulic properties of stems (GARTNER, 1991), but it is one way of enhancing water transport. High HV in EG may be related to mechanical support of their sclerophylls leaves, but in the DC *B. cumanensis* it appears to point to a larger investment in conducting tissue. Nonetheless, the HV of these DC and EG were lower, compared to other tropical species (TYREE *et al.*, 1991; MACHADO & TYREE, 1994; SOBRADO, 1996).

EG are inefficient in water transport relative to DC, however both embolize at comparable xylem tensions. This means that species with less efficient water

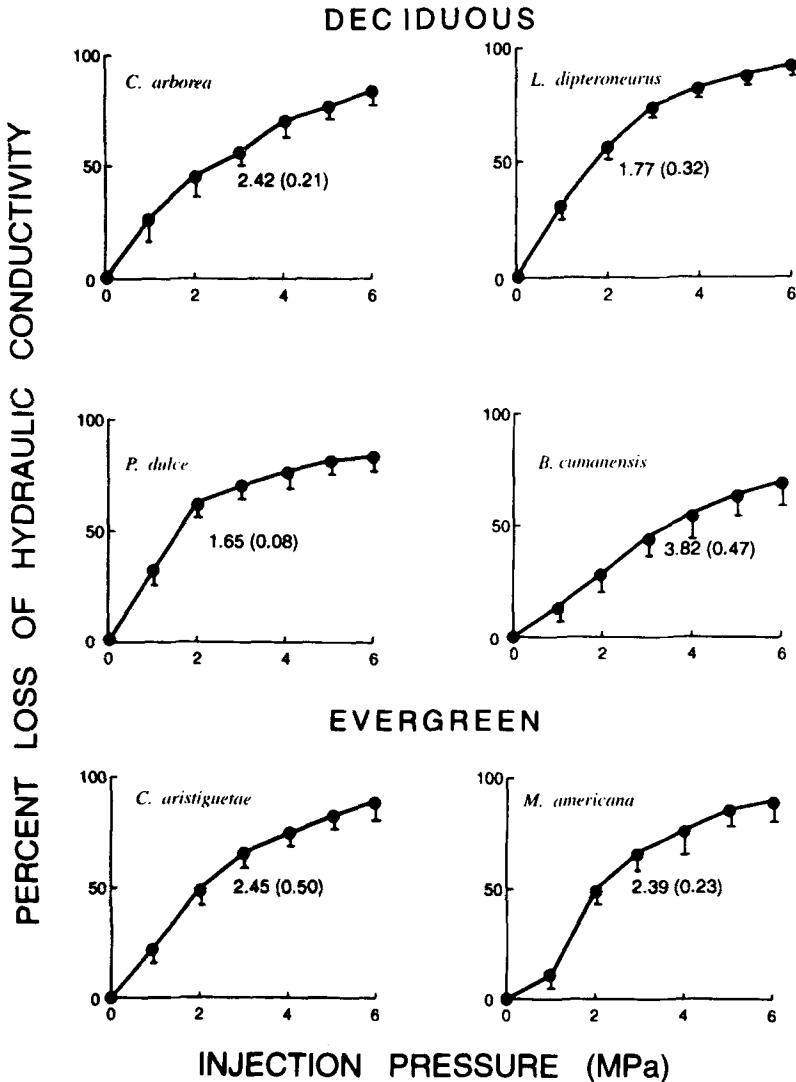


FIG. 1. – Percentage loss of hydraulic conductivity, due to pressure-induced embolisms, as a function of air injection pressure (cavitation tension) measured in four drought-deciduous and two evergreen species. Each value represents the mean \pm standard errors of six replicate stem-segments, 22 cm long and 5-7 mm diameter, taken during the wet season. Values under curves represent the mean pressures (standard error) at 50 percent loss of hydraulic conductivity. Least significant difference at $p < 0.05$ was 0.59.

transport are not necessarily less at risk from xylem dysfunction (TYREE *et al.*, 1995). Therefore, there is little margin of safety against catastrophic loss of hydraulic conductivity in both DC and EG. Overall, seasonal differences indicated that most PLC occurred in DC during the dry season. This is in accordance with

the lower stem water content and the high wood specific gravities of DC during this period in seasonally dry tropical forests (SCHULZE *et al.*, 1988; SOBRADO, 1993, 1995; BORCHERT, 1994b).

Despite some differences in the magnitude of the response, the shape of the vulnerability-curves were very similar among the six species. A rapid increase in vulnerability at high water potential (<injection pressure) is followed by a slow response at low water potential (>injection pressure). Permeability of pit membranes sets the embolism threshold of the vascular system, and these membranes are the sites where the threshold can be regulated (SPERRY *et al.*, 1991; COCHARD *et al.*, 1992). Differences in pit permeability of these DC and EG may be small. However, a given species may contain a range of vessel diameters with different pit permeability (SPERRY *et al.*, 1991). The vessels with high pit conductance are more efficient for water conduction but also are at a higher risk from embolism.

Overall, vulnerability curves seem to reflect the range of stem xylem pressure the species experiences in nature (SPERRY *et al.*, 1987). The trend for species vulnerability following test of significance ($p < 0.05$) was *Lonchocarpus dipteroneurus* = *Pithecellobium dulce* > *Coursetia arborea* = *Capparis aristiguetae* = *Morisonia americana* > *Beureria cumanensis*. Furthermore, the Vulnerability Index (vessel diameter/vessel number per mm²), which is indicative of the conductive safety of wood (CARLQUIST, 1977), is 0.68 in *B. cumanensis* compared to 1.60 and 1.70 in evergreen *Capparidaceae* species and deciduous *Pithecellobium* species, respectively (LINDORF, 1994). This is a consequence of more (68 vessels/mm²) narrow vessels (46 μ m diameter) in *B. cumanensis* than in *Capparidaceae* (45 vessels/mm²; 72 μ m) and *Pithecellobium* (38 vessels/mm²; 63 μ m) species. Xylem dysfunction due to embolism at modest tension may reduce the rates of water extraction and prolong water availability during drought (SPERRY & SALIENDRA, 1994). The presence of a higher resistance to xylem embolism in *B. cumanensis* would, in theory, allow this species to resist lower stem water potential better than the other species. It is worth noting that this tree is the phytosociologically dominant one in this forest and its leaves have later senescence during drought (SOBRADO, 1991). In general, xylem susceptibility to water-stress-induced embolism was lower here than has been found in other tropical species from more humid areas (MACHADO & TYREE, 1994; ZOTZ *et al.*, 1994; SOBRADO, 1996).

Low leaf water potential has been measured with a pressure chamber in both DC and EG species on a diurnal or seasonal basis (SOBRADO & CUENCA, 1979; SOBRADO, 1986). This may imply that both DC and EG are under the same risk from suffering runaway embolisms in both plant types. Despite the fact that the occurrence of embolisms has been related to the water potential of the leaves, it is recognized that water potential of the stems will be somewhat higher (JONES & SUTHERLAND, 1991). In tropical dry forests, however, the difference between stem and leaf water potentials in DC are very small, but they can be up to 3 MPa in EG (BORCHERT, 1994b). Thus, we suspect that large leaf hydraulic resistance may occur in sclerophylls EG and this would confine low water potential to the leaf but not to stems. In fact, leaves of the EG *M. americana* and *C. aristiguetae* appear to be adapted to large water deficits: They undergo a very large drop in water potentials before turgor loss (SOBRADO, 1986). The role of leaf hydraulic resistance in the water relations of these DC and EG is unknown and is a potentially worthy subject for investigation.

In conclusion, the degree of embolism in DC and EG was not determined by differences in vulnerability curves. Moreover, no interrelation was found between xylem efficiency in terms of KI and tension at 50 PLC embolisms, indicating that susceptibility to embolisms is independent of the conducting efficiency. However, there is a strong link between foliar phenology and the degree of seasonal xylem embolisms: EG accumulated fewer embolisms by the end of the dry season than DC. The threat of runaway embolism may be better ameliorated in EG than in DC due to their ample water supply from deeper roots (SOBRADO & CUENCA, 1979; SOBRADO & EHLERINGER, 1997) and their conservative water use caused by a lower transport efficiency. Differences in root depth and water availability between DC and EG seemed to be the underlying cause of embolism numbers as well as of phenological patterns observed in this tropical dry forest. Notwithstanding, the occurrence of a lower susceptibility to drought-induced embolisms in *B. cumanensis* implied that risk from xylem dysfunction may have some ecological significance with respect to the dominance of this species in the ecosystem.

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