

Vulnerability to drought-induced embolism of Bornean heath and dipterocarp forest trees

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Summary Occasional droughts may be important in controlling the distribution and structure of forest types in relatively aseasonal north Borneo. The low water retention capacity of the coarse, sandy soils on which tropical heath forest occurs may cause drought to develop more quickly and severely than on the finer textured soils of nearby dipterocarp forest. Resistance to drought-induced embolism is considered an important component of drought tolerance. We constructed embolism vulnerability curves relating loss in hydraulic conductivity to xylem tension by the air-injection method for understory trees of 14 species from both tropical heath and mixed dipterocarp forests in Brunei Darussalam. There was no significant difference (Mann-Whitney *U*-test, $P = 0.11$) between forest types in the xylem tension at which 50% loss of hydraulic conductivity occurred. Most species from both forest types were highly vulnerable to embolism compared with species from seasonal tropical forests. We speculate that other mechanisms, such as stomatal control to prevent development of embolism-inducing xylem tensions, are more cost-effective adaptations against occasional drought, but that the attendant reduction in productivity and competitive ability places a greater premium on resistance to embolism when drought is annual and predictable.

Keywords: *air-injection technique, tropical forest, water stress.*

Introduction

The importance of drought in shaping the structure and dynamics of seasonal and even aseasonal tropical forests is increasingly appreciated (Brunig 1974, Condit et al. 1995, Burslem et al. 1996, Newbery et al. 1996, Walsh 1996, Becker et al. 1998a). In relatively aseasonal north Borneo, analysis of daily rainfall has revealed the occurrence of supra-annual drought obscured by monthly averages (Brunig 1969, Becker 1992). Whether plants experience significant water stress during such droughts depends on soil water capacity, and hence soil depth and texture and plant rooting depth (Brunig 1971, Baillie 1976).

Water stress is thought to play a role in the distribution and structure of forest types in north Borneo (Brunig 1974).

Physiognomically and floristically distinct heath forest typically grows on coarse, sandy soils with low water and nutrient retention capacity, whereas taller, more species-rich dipterocarp forest is found on finer textured soils (Whitmore 1984). Taking account of evapotranspiration rate and field capacity, exhaustion of the soil water store was estimated to occur after > 100 rainless days for dipterocarp forest and in half that time for heath forest on deep soils (Bruenig 1996).

Plants that experience water stress should show morphological and physiological adaptations to mitigate its negative impact on their growth and reproduction. Xylem cavitation and embolism, caused by air sucked into conduits at high water tension, is not rare, nor is it confined to severely droughted plants (Grace 1993). Loss of a critical amount of conductance capacity, however, can trigger runaway embolism and a total failure of the water transport system. Stomatal closure is the first line of defense against such an event (Tyree and Sperry 1988, Jones and Sutherland 1991). Although the sufficiency of the cohesion-tension theory for the ascent of xylem water has been questioned (e.g., Zimmermann et al. 1995), much evidence supports the existence of high tensions (low water potentials) in the xylem (e.g., Steudle 1995, Tyree 1997).

Tyree and Ewers (1991) considered the resistance of the xylem to cavitation to be an important parameter determining drought resistance, with long-lived trees being limited by the minimum soil water potential reached during severe droughts occurring at decadal intervals. They suggested that the ecological distribution of some plants is affected by either their ability to withstand embolism or to recover from it. The vulnerability of xylem to embolism across taxa correlates with the minimum xylem pressures that they develop, with the safety margin against complete failure of water transport being least in plants that develop less negative pressures (Sperry 1995). The development of severe embolism during natural drought is well documented (e.g., Cochard et al. 1992b, Tognetti et al. 1996). Several months after the rains returned following a strong drought in Brunei during 1993, some understory trees from both heath and dipterocarp forests failed to restore sap flow in presumably embolized bole regions (P. Becker, unpublished data) although at least partial recovery occurred in canopy trees (Becker 1996).

Here we report the results of a broad comparative survey of vulnerability to embolism in trees from heath and dipterocarp forests experiencing the same climate in Brunei. We predicted that species from heath forest would be less vulnerable to embolism than species from dipterocarp forest. We studied those species making the greatest contribution to stand basal area on the assumption that this would best indicate possible evolutionary trends differentiating these forests with respect to their water relations, and because such species have the greatest impact on forest function and dynamics. To place our results in a broader context, we compare them with published data on embolism vulnerability of species from tropical forests experiencing a regular dry season.

To characterize the susceptibility of a species to embolism, vulnerability curves showing the relationship between hydraulic conductivity and xylem pressure are constructed (Sperry et al. 1988). Vulnerability to embolism is governed by pit membrane pore size in vessels or the displacement of the aspirated torus sealed against the overarching border of the pit in tracheids. These are the entry paths of the air initiating cavitation (Sperry and Tyree 1990). The same vulnerability curve is obtained whether embolism is induced by negative xylem pressure in dehydrated stems, or by positive air pressure injected into the vascular system of hydrated stems (Alder et al. 1996 and references therein). We elected to use the more convenient air-injection procedure, which still requires at least three days to complete a vulnerability curve for one species, including replicate samples of plant material.

Methods

Study sites and species selection

Plant material was collected from a mixed dipterocarp forest at Andulau Forest Reserve (4.66° N, 114.52° E, 37–59 m a.s.l.) and from a tropical heath forest at Badas Forest Reserve (4.57° N, 114.41° E, 11–16 m a.s.l.) in Brunei Darussalam. Annual rainfall is about 3000 mm in both forests, and periods when the 30-day total of rainfall remained less than 100 mm for more than a month have occurred about once every two years (Becker 1992). Davies and Becker (1996) provide a detailed description of the soils, stand structure, and floristic composition of the 0.96-ha study plots. Briefly, the dipterocarp forest occurs on loamy sands exceeding 1-m depth with moderate slopes, whereas the heath forest is on a terrace comprising a bleached sand overlying an indurated humic horizon at 2-m depth. The tree size class distribution of the two forests is similar, except that stems of 0.01–0.05 m dbh (diameter at 1.3 m aboveground) are twice as abundant in the heath forest as in the dipterocarp forest. The heath forest plot (113 species) has less than one-third as many species as the dipterocarp forest plot (393 species) and is strongly dominated by the conifer *Agathis borneensis* V. Sl.

At each site, 14 species were selected for study from among the 55 species at Andulau and the 31 species at Badas making the largest contributions to stand basal area (Table 1). An additional criterion was that the species also be represented by small trees (0.05–0.13 m dbh) in the understory. Small trees

were studied because of their accessibility and because trees in the 0.01–0.05 m dbh size range were found to be most vulnerable to drought-induced mortality at Badas (Becker and Wong 1993).

Vulnerability to xylem embolism

Branches of 1–2 m length were collected during a wet period (November 1995 to May 1996) and brought to the laboratory in moistened plastic bags for the air-injection experiments. After storage for ≤ 3 days, straight segments 320–460 mm in length and 5–17 mm in diameter were cut under water to remove vessels blocked with air during harvesting. The stem segment was connected to an air-water pressure tank and flushed for 60 s in both directions with distilled, degassed, filtered (0.1 μm) water at a pressure gradually increasing to 200 kPa to remove air that had entered the stem during manipulation. Previous studies have shown that hydraulic conductivity is only slightly dependent on stem length, provided that the ends are not plugged (M.T. Tyree, unpublished data).

Vulnerability of xylem to embolism was measured by the injection technique (Cochard et al. 1992a). A stem segment was enclosed in a steel chamber with its ends protruding through a rubber seal to the outside air. Filtered, distilled and degassed water was forced at 4 kPa through the stem from the natural upstream end and collected at the downstream end by tubing leading to a container on an electronic balance. This pressure was too low to displace air from any embolized vessels that were open at both ends of the segment. Initial hydraulic conductivity, k_i , was determined from the mass flow rate divided by the pressure gradient across the segment.

The stem was then embolized by pressurizing the chamber to force air into the vascular system through a debarked strip 100-mm long in the middle of the stem. The stem was disconnected from the conductivity apparatus and held for 40 min at the selected gas pressure. Air pressure inside the xylem conduits was then allowed to equilibrate for 10–180 min, depending on stem diameter and density. During equilibration, air in the injection chamber was lowered to atmospheric pressure, and the upstream end of the segment was immersed in water to prevent drying. After equilibration, hydraulic conductivity, k_h , was measured with the chamber at atmospheric pressure. The degree of embolism was calculated as the percentage loss in conductivity relative to its initial value [$100(k_i - k_h)/k_i$]. This process was repeated four to six times with increasing air pressures until 80–100% loss of initial conductivity was reached.

Vulnerability curves were obtained by plotting percent loss of hydraulic conductivity (L) against injection pressure (P) for 3–8 stem segments from 1–4 trees of each species. These curves were well-fit (raw $R^2 = 0.82$ – 0.99) by the sigmoid equation:

$$L = \frac{100}{1 + \exp(a(P - b))}, \quad (1)$$

where a measures how strongly conductivity responds to injection pressure (curve shape), and b indicates the pressure at

Table 1. Species studied from dipterocarp and heath forests, their contribution to total basal area in the 0.96-ha plots (for all trees ≥ 0.05 m dbh), and the coefficients of Equation 1 fitted to their vulnerability curves. The negative of $b = \Psi_{50\text{PLC}}$, the xylem tension causing 50% loss of hydraulic conductivity. Values of b exceeding 1 are shown in bold. Nomenclature as in Davies and Becker (1996).

Species	Family	% Basal area	a	b
Dipterocarp forest				
<i>Dryobalanops aromatica</i> Gaertn. f.	Dipterocarpaceae	7.5	-10.3	0.26
<i>Shorea mecistopteryx</i> Ridl.	Dipterocarpaceae	5.5	-7.4	0.63
<i>Shorea faguetiana</i> Heim.	Dipterocarpaceae	5.4	-4.6	0.37
<i>Dipterocarpus globosus</i> Vesque	Dipterocarpaceae	4.0	-11.7	0.18
<i>Pentace adenophora</i> Kosterm.	Tiliaceae	4.0	-8.6	0.19
<i>Amyma pluricornis</i> (Radlk.) Domke	Thymelaeaceae	3.3	-2.3	0.63
<i>Shorea ovalis</i> (Korth.) Bl.	Dipterocarpaceae	2.2	-8.3	0.39
<i>Santiria mollis</i> Engl.	Burseraceae	1.7	-4.9	0.20
<i>Lophopetalum subobovatum</i> King	Celastraceae	1.5	-3.7	0.59
<i>Payena endertii</i> H.J. Lam	Sapotaceae	0.7	-3.9	0.63
<i>Diospyros brachiata</i> K. & G.	Ebenaceae	0.6	-3.9	0.42
<i>Heritiera sumatrana</i> (Miq.) Kosterm.	Sterculiaceae	0.4	-2.3	1.69
<i>Mallotus wrayi</i> King ex Hook f.	Euphorbiaceae	0.4	-6.5	0.53
<i>Diospyros</i> cf. <i>mindanaensis</i> Merr.	Ebenaceae	0.4	-5.5	0.79
Heath forest				
<i>Agathis borneensis</i> V. Sl.	Araucariaceae	64.6	-1.7	1.91
<i>Corylelobium burckii</i> Heim.	Dipterocarpaceae	5.5	-10.2	0.45
<i>Eugenia bankensis</i> (Hassk.) Backer	Myrtaceae	4.8	-1.3	1.26
<i>Nephelium lappaceum</i> Linn.	Sapindaceae	1.4	-3.4	0.76
<i>Eugenia muelleri</i> Miq.	Myrtaceae	1.1	-6.2	0.54
<i>Aglaia glabrata</i> Teijsm. & Binn.	Meliaceae	1.0	-2.6	0.71
<i>Canarium caudatum</i> King	Burseraceae	0.9	-1.5	1.47
<i>Isonandra lanceolata</i> Wight	Sapotaceae	0.9	-5.1	0.48
<i>Stemonurus umbellatus</i> Becc.	Icacinaceae	0.7	-2.6	0.18
<i>Eugenia</i> cf. <i>ampullaria</i> Stapf.	Myrtaceae	0.6	-9.3	0.60
<i>Homalium moultonii</i> Merr.	Flacourtiaceae	0.4	-0.5	6.3
<i>Diospyros hermaphroditica</i> (Zoll.) Bakh.	Ebenaceae	0.4	-4.2	0.60
<i>Xerospermum laevigatum</i> Radlk.	Sapindaceae	0.4	-15.7	0.18
<i>Sindora leiocarpa</i> Backer ex de Wit	Fabaceae	0.3	-3.4	0.86

which 50% loss of conductivity occurs (curve displacement along the x -axis) and does not affect curve shape. See Pammenter and Vander Willigen (1998) for a detailed discussion of the behavior and interpretation of this equation. Because embolisms are induced under natural conditions by tensions in the xylem, the vulnerability curves shown here are plotted with the negative of injection pressure. The coefficients a and b were estimated by a nonlinear, least squares, quasi-Newton method confirmed by a simplex procedure. This and all other statistical and graphical analyses were performed with SYSTAT 5.03 (SYSTAT, Inc., Evanston, IL).

Results

There were large differences among species both in variation of observed values about the fitted vulnerability curve and the coefficients characterizing that curve, but Equation 1 proved a useful descriptive model (Figure 1). The coefficients a and b are intrinsically positively correlated, and the relationship is curvilinear because a given change in a increasingly affects curve shape as a approaches zero (Figure 2).

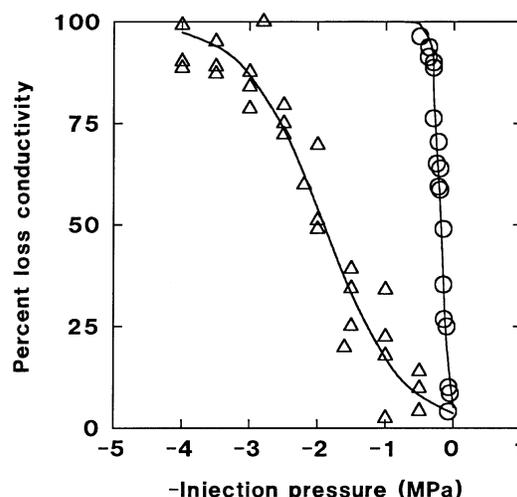


Figure 1. Curves for *Agathis borneensis* (Δ) and *Xerospermum laevigatum* (\circ) illustrating extremes (excluding *Homalium moultonii*) of vulnerability to embolism and its variability at a given air-injection pressure. Lines are nonlinear least squares fits of Equation 1 yielding coefficients in Table 1.

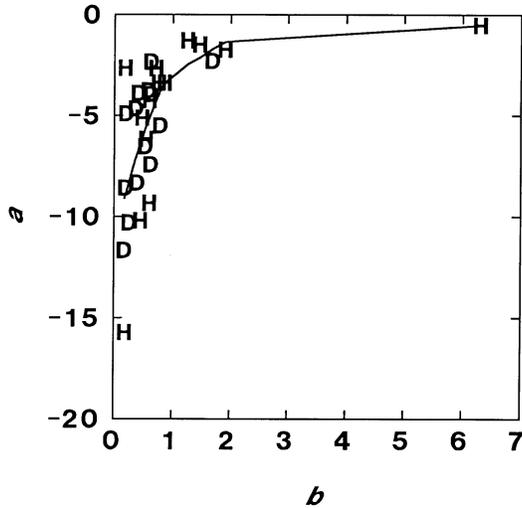


Figure 2. Nonlinear correlation between coefficients of Equation 1 fitted to vulnerability data of 14 tree species from dipterocarp (D) and heath (H) forests. Line fitted by lowess (tension = 0.7).

Most species from both heath and dipterocarp forests were highly vulnerable to embolism compared with previous measurements of tropical and temperate species (Tyree et al. 1994a). Vulnerability was apparently unrelated to a species' contribution to stand basal area (Table 1) or its topographic preference (data not shown). There was no statistically significant difference in vulnerability to embolism between forest types as measured by the coefficients a and b (Table 1, Mann-Whitney U -tests, $P = 0.14$ and 0.11 , respectively). Consistent with our prediction, more species from heath forest than from dipterocarp forest showed moderate to low vulnerability to embolism ($b > 1$ in Table 1, Figure 2). Nevertheless, in their vulnerability to embolism, the heath forest species were more similar to species from aseasonal dipterocarp forest than to other tropical species experiencing a distinct dry season (Figure 3).

Discussion

Eleven out of 28 species studied from heath and dipterocarp forests had $> 50\%$ loss of conductivity at air-injection pressures of 0.5 MPa, indicating that they are among the species most vulnerable to cavitation. This means that xylem pressures cannot drop much below -0.5 MPa in stems of these species if total failure of the water transport system to subtended tissue is to be avoided. However, leaf water potentials could be much more negative if smaller diameter stems and leaves are less vulnerable than the stems measured in this study. Preliminary observations on small saplings in heath forest, which are presumably more shallow rooted and therefore more susceptible to soil water stress than the trees studied here, suggest that strong stomatal control enables fairly high water potentials to be maintained during drought (Becker et al., unpublished data).

Climate was more important than soil type in determining

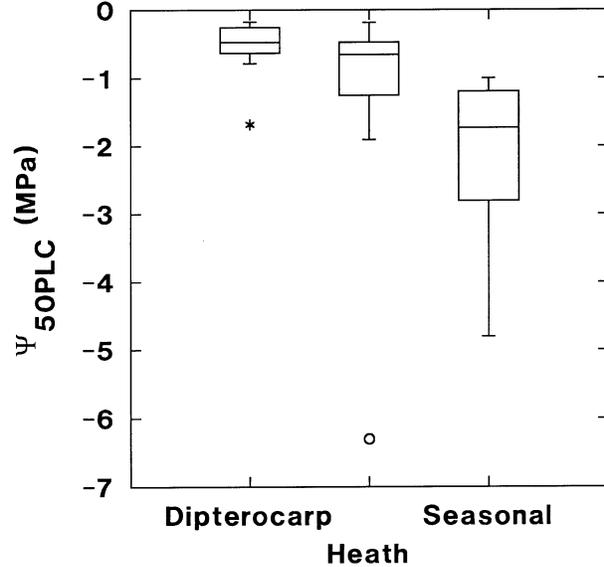


Figure 3. Xylem tension causing 50% loss of hydraulic conductivity (Ψ_{50PLC}) for 14 tree species from both dipterocarp and heath forests (present study) and 12 tree species from seasonal forests. The latter include deciduous and evergreen species from young semi-evergreen forest in Panamá (Tyree et al. 1994a) and tropical dry forest or savanna in Venezuela (Sobrado 1996, 1997). Box plots show median (central horizontal line), interquartile range (box), and range (whiskers) exclusive of extreme values (circle or star).

the characteristic vulnerability to embolism of the tropical forest types compared here. Severe drought is infrequent and unpredictable for both heath and dipterocarp forest at our northern Borneo study sites, whereas the seasonal forests of Panamá and Venezuela experience annual dry seasons of four to six months duration (Becker 1992; M.A. Sobrado, Universidad Simon Bolivar, Caracas, Venezuela, personal communication). Strong stomatal control to prevent the development of excess xylem tension may be an effective mechanism to prevent embolism during occasional drought, but the attendant reduced productivity and competitive ability makes this a less viable response in seasonal climates. Analysis of the cost of low vulnerability is complex. There is a weak but significant correlation between vessel diameter (a measure of hydraulic efficiency) and vulnerability to embolism, indicating a trend of evolutionary importance. Deviations from the trend can be understood in terms of the seeding mechanism of xylem embolism (see Tyree et al. 1994a for details).

The apparent unimportance of soil type may be explained by recent modeling (Sperry et al. 1998) which suggests that, for plants on coarse soils (as in our heath and dipterocarp forests), loss of conductivity at the soil-root interface occurs at water potentials above those that would cause runaway embolism. Thus, resistance to embolism would offer no advantage if the xylem is not the weak link in the soil-plant-atmosphere continuum. Available water in heath soils may also have been underestimated (cf. Bruenig 1996). Recent observations in the Badas heath forest on a deep humus podzol indicated that extractable water in the top 1.2 m of soil was almost depleted

after 35 nearly rainless days, but there were still substantial water reserves above the hardpan at 2-m depth even after two months (P. Becker, unpublished data).

Even species from arid climates show large differences in vulnerability to xylem embolism. Thus, such vulnerability cannot be the sole index of water stress tolerance, which should be viewed as a highly coordinated, whole-plant process (Kolb and Davis 1994). Comparisons of the wood anatomy of xeric and mesic floras indicate that the tendency for higher conductive efficiency of species growing in dry areas is at least as strong as the tendency for increased hydraulic safety (Baas 1986). Pockman et al. (1995) noted that, although the mechanism and occurrence of embolism are fairly well documented, its significance for determining drought tolerance and habitat preference is less well understood. Embolization need not have entirely negative consequences. Partial embolism may be beneficial in reducing demand on soil water during rainless periods (Alder et al. 1996). However, realization of such an advantage will depend on whether the rooting volume of a plant is penetrated by strongly water-demanding roots of other plants. Severe embolization may lead to the shedding of vulnerable and easily replaced organs, such as terminal shoots and leaves, to preserve plant components essential for regeneration (Tyree et al. 1993b).

Several mechanisms besides stomatal control of transpiration have been proposed to compensate for high vulnerability to embolism. Stored water in stems could be important during drought by helping to buffer water potential (Tyree and Yang 1990, Tognetti et al. 1996). A dynamic model of water flow in a tropical tree indicated that its high leaf specific conductivity (mass flow rate per pressure gradient per leaf area) required only a small drop in stem xylem pressure potential to draw water up to the leaves, thereby maintaining xylem water potential at values unlikely to cause cavitation (Tyree et al. 1991). Based on the findings that deep roots enable highly vulnerable *Populus* spp. to grow in semi-arid regions (Tyree et al. 1994b) and that many saplings and some small trees and shrubs of both dipterocarp and heath forests are deep-rooted (Becker et al. 1998b; J. Grainger, University of Cambridge, U.K. and P. Becker, unpublished data), we postulate that deep rooting is mainly an adaptation to occasional drought. However, species that are not deep rooting also have mechanisms for withstanding drought. For example, the shallow-rooted shrub *Piper cordulatum* C. DC. is able to maintain water potentials above its turgor loss point throughout the dry season by exercising strong stomatal control (Rundel and Becker 1987). Thus, for each species, it is the whole-plant response to drought that is important.

We note that the small branches from which vulnerability curves are typically constructed represent only a fraction of the whole-tree resistance to water flux (Tyree et al. 1993a). There is evidence that root xylem is usually more vulnerable to embolism than stem xylem (Kolb et al. 1996, but cf. Tsuda and Tyree 1997) and so may be a more sensitive indicator of drought tolerance (Alder et al. 1996). Roots of the riparian *Betula occidentalis* Hook. were substantially embolized (in response to midday water stress), whereas trunks and twigs remained nearly maximally conductive (Sperry and Saliendra

1994). We speculate that differences in species composition, and hence structure, between dipterocarp and heath forest arise at the seedling establishment stage because shallow-rooted seedlings are especially prone to water stress.

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