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A survey of root pressures in vines of a tropical lowland forest

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Abstract Pre-dawn xylem pressures were measured with bubble manometers attached near the stem bases of 32 species of vines on Barro Colorado Island, Panama, to determine if pressures were sufficient to allow for possible refilling of embolized vessels. Of 29 dicotyledonous species 26 exhibited only negative xylem pressures, even pre-dawn during the wet season. In contrast, three members of the Dilleniaceae exhibited positive pre-dawn xylem pressures, with a maximum of 64 kPa in *Doliocarpus major*. A pressure of 64 kPa is sufficient to push water to a height of 6.4 m against gravity, but the specimens reached heights of 18 m. Thus, in all 29 dicotyledons examined, the xylem pressures were not sufficient to refill embolized vessels in the upper stems. In contrast, two of the smaller, non-dicotyledonous vines, the climbing fern *Lygodium venustrum* and the viny bamboo *Rhipidocladum racemiflorum*, had xylem pressures sufficient to push water to the apex of the plants. Therefore, a root pressure mechanism to reverse embolisms in stem xylem could apply to some but not to most of the climbing plants that were studied.

Key words Lianas · Vines · Root pressure · Xylem water potential · Barro Colorado Island

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Introduction

Lianas (woody vines) are much more common in tropical than temperate ecosystems, but the reasons for this are unknown (Gentry 1991). Lianas have long been known to have thin stems and a high ratio of leaf area to transverse stem area (Schenck 1893; Hallé et al. 1978; Putz 1983; Ewers and Fisher 1991). Wide xylem vessels, which in temperate areas are quite prone to freezing-induced embolism (Cochard and Tyree 1990; Sperry and Sullivan 1992; Sperry et al. 1994), are also one of the characteristic features of tropical lianas (Berger 1931; Huber 1956; Zimmermann and Brown 1971; Carlquist 1975; Ewers et al. 1990; Ewers and Fisher 1991). It is not known whether the wide vessels of tropical vines usually avoid embolism throughout the life of the stems, or if they become embolized and are periodically refilled. If a perennial plant such as a liana could not refill its embolized vessels, its distribution might be limited to environments where embolism induction would be minimal. For instance, some species might be limited to environments with a very consistent water supply and without freezing temperatures.

Positive xylem pressures in the stems of plants usually are attributed to "root pressure", i.e., the osmotic water uptake caused by solute uptake into roots (Tyree et al. 1994b). The water flow caused by root pressure is normally much less than that caused by transpiration pull. When transpiration is high, the osmotic force causing root pressure tends to disappear because solutes are diluted by an influx of soil water as evaporative pull increases tension (negative pressure) in the xylem water. Thus root pressure is highest when transpiration is minimal, such as pre-dawn and during rainstorms (Cochard et al. 1994).

Tropical palm trees have been reported to have root pressures sufficient to pump water up to heights as great as 12.5 m (Davis 1961) and there is evidence that at least some tropical lianas have positive water pressure in their stem xylem at certain times (Scholander et al. 1957; Putz

1983). Since the wide vessels of tropical liana stems remain conductive for many years, it has been suggested that they might be refilled (= reversal of air embolism) as a result of root pressure sufficient to dissolve emboli in vessels (Putz 1983; Ewers et al. 1991).

The physical conditions permitting gas dissolution in water are well understood. Henry's law states that the gas solubility in water is proportional to the gas pressure adjacent to the water. Since plants are surrounded by air at atmospheric pressure, we can assume that water in plants is nearly saturated with gas at the concentration demanded by Henry's law. Applying Henry's law in reverse, we can conclude that any void in a vessel will also become filled with air at atmospheric pressure, otherwise it would not be in equilibrium with the gas in water. Therefore, the only known way that an embolism can dissolve is if gas pressure is above atmospheric. This condition can be achieved, for instance, by the compressive force of root pressure and by the surface tension of the bubble. Surface tension can increase the pressure on a bubble above the fluid pressure, with the amount of added pressure being inversely proportional to bubble diameter.

The time required for dissolution of an embolism is positively correlated with xylem pressure (P_x) and inversely correlated with vessel diameter (D, μm). The critical fluid pressure for embolism reversal (P_c), that is, the minimum pressure required to dissolve an embolism, given sufficient time, is

$$P_c = -4\tau/D \tag{1}$$

where τ is the surface tension of water (Tyree and Yang 1992; Tyree et al. 1994a). When P_x exceeds $-4\tau/D = -284$ kPa μm/D (at 25°C; Tyree et al. 1994a), the air in the embolism is above atmospheric pressure and can dissolve as dictated by Henry's law. In the present study atmospheric pressure is assumed to be equal to 0 kPa. For a vessel of $D = 200$ μm, it can be seen that P_x must exceed $P_c = -1.4$ kPa adjacent to the embolism.

However, P_x near a bubble at height h will be less than the root pressure measured at the base of the plant (P_{xb}) because of gravitational effects on pressure (see Yang and Tyree 1992; Lewis et al. 1994). Since roots have to push water against a gravity gradient of -10 kPa m^{-1}, the critical height for the dissolution of an embolism (h_c, m), that is, the maximum height for embolism reversal assuming equilibrium static conditions, will be

$$h_c = (P_{xb} - P_c)/10 \tag{2}$$

For example, for the 200-μm-diameter vessel, P_x will exceed P_c near a bubble at 10 m above soil level only when $P_{xb} > 98.6$ kPa.

Positive P_x values sufficient to dissolve emboli have been demonstrated in the temperate lianas *Vitis labrusca* and *V. riparia*. Refilling occurs in these species when the plants are in a leafless condition in spring, thus minimizing the loss of water from transpiration (Sperry et al. 1987).

The present study was designed to test the hypothesis by Putz (1983) that root pressures might be sufficient to refill embolized vessels in tropical lianas. To this end we measured pre-dawn P_{xb} and vessel diameters of 32 species of vines in a tropical lowland forest, during both the dry and wet seasons. Root-climbing species, that is, plants such as members of the Araceae that climb using adventitious roots to adhere to the host plant, were not included.

Materials and methods

All the surveyed plants were growing in a 40 × 80 m (projected area) plot, with a 25% east-facing slope, on Barro Colorado Island, Panama. Destructive sampling was permitted because the site was designated for the building of a new research laboratory. The plot, with a canopy height of 18 m, was an excellent site for vine biodiversity because it was a young forest site that had been cleared 50 years earlier and because it was surrounded by a large gap that allowed proliferation of lianas near the edges of the plot.

We studied all vine species on the plot that were identifiable, excluding root climbers. Root pressure observations and measurements were made on 65 individuals of 32 species of climbing plants, including 20 genera from 13 families (Table 1). Voucher specimens for each species are deposited in the Michigan State University (MSC) herbarium. Nomenclature follows Croat (1978) and, for *Clitoria falcata*, Dwyer (1980).

Pre-dawn xylem pressures were measured in 1992 during both the late dry season and during the mid-wet season. Prior to/during the dry season measurements, 33 mm, 3 mm, and 10 mm of rain fell during January, February, and March, respectively, and no rain fell between 18 March and 6 April, when all the dry season measurements were made. In contrast, prior to/during the wet season measurements, 306 mm, 434 mm, and 438 mm of rain fell during August, September, and October, respectively, and it rained almost every day between 9 and 22 October, when all the wet-season measurements were made.

Previous studies and preliminary results indicated that maximum P_x values would occur at pre-dawn (Sperry et al. 1987; Cochard et al. 1994). The initial observations on each plant were confined to evidence of predawn exudation (see below), which is qualitative evidence of positive pressure. When exudation did occur, bubble manometers were installed in the evening to allow for quantitative measurements before the next sunrise.

Exudation was observed at predawn by cutting off a lateral branch (or leaf stipe in the case of *L. venustrum*) with a clipper within 2 m from the soil surface, usually at about 0.5 m. In some cases, where lateral branches were not available, the main stems were cut near the base. Observations were made on the remaining stump with a hand lens and flashlight. If exudation occurred, the surface was dried with a towel to confirm continued exudation from the xylem. Plants that failed to exude always failed to show positive predawn xylem pressure as measured with a manometer.

Xylem pressure measurements were made with bubble manometers that were attached to the branch stumps. The manometers were made from glass tubes (1 mm internal diameter) and were sealed at the distal end by flame. The distal half was filled with air while water filled the basal half. The base was connected to the stump by a tight fitting vinyl tube and hose clamps. Prior to attachment, the freshly cut stump was shaved with a new razor blade to permit unobstructed fluid flow between the stump and manometer. Each evening the cut stumps were reshaved and the manometers reattached. After allowing for equilibration overnight, the bubble length (L_{pd}) in the manometer was measured at predawn. The vinyl tubing was then cut and the bubble length (L_{atm}) immediately remeasured at atmospheric pressure. The xylem water pressure (P_x in kPa) was calculated from a relation derived from the ideal gas law:

Table 1 Maximum pre-dawn xylem pressures (Ψ in kPa) for climbing plants on Barro Colorado Island, Panama. Assumes atmospheric pressure = 0 kPa;– indicates negative pre-dawn xylem pressures. (*F* leaf-climbing fern, *M* "semi-woody" monocotyledonous vine, *V* her-baceous dicotyledonous vine, *L* dicotyledonous liana, *H* semi-woody hemiepiphyte)

Taxon (Voucher no.)	Growth form	Max. xylem Ψ (kPa)	No. of individuals
PTEROPHYTA			
Schizaeaceae			
Lygodium venustrum Sw. (12,66,66B,68)	F	66	4
ANTHOPHYTA			
MONOCOTYLEDONEAE			
Poaceae			
Rhipidocladum racemiflorum (Steud.) McClure (30)	M	120	1
Smilacaceae			
Smilax panamensis Morong (62)	M	–	1
DICOTYLEDONEAE			
Asteraceae			
Mikania leiostachya Benth. (53)	V	–	1
Bignoniaceae			
Arrabidaea candicans (L.C. Rich.) DC (61)	L	–	1
A. chica (H.&B.) Verl. (43,69)	L	–	2
A. patellifera (Schlecht.) Sandw. (27)	L	–	1
Phryganocydia corymbosa (Vent.) Bur. ex K. Schum. (58)	L	–	1
Stizophyllum riparium (H.B.K.) Sandw. (51)	L	–	1
Boraginaceae			
Tournefortia cuspidata H.B.K. (18,48)	L	–	2
Combretaceae			
Combretum decandrum Jacq. (14,36,70)	L	–	3
Dilleniaceae			
Doliocarpus dentatus (Aubl.) Standl. (59)	L	–	1
D. major J.F. Gmel. (25,44)	L	64	2
D. olivaceus Sprague & L.O. Wms. ex Standl. (16)	L	–	1
Tetracera hydrophila Tr. & Planch. (1, 1B,6)	L	16	3
T. portobellensis Beurl. (34, 38, 39,60)	L	57	4
Fabaceae, subfamily Papilionoideae			
Clitoria falcata Lam. (49)	L	–	1
C. javitensis H.B.K. (4,8,26,29,45)	L	–	5
Dalbergia brownei (Jacq.) Urban. (54)	L	–	1
Machaerium kegelii Meisn. (67)	L	–	1
M. microphyllum (E. Meyer) Standl. (28,52,55,57,67)	L	–	5
M. milleflorum Pitt. (22,22B,31,33,37,41,42,55)	L	–	8
Gesneriaceae			
Drymonia serrulata (Jacq.) Mart. (65,73)	H	–	2
Malpighiaceae			
Stigmaphyllon ellipticum (H.B.K.) Adr. Juss. (7)	L	–	1
Hiraea faginea (Sw.) Niedenzu (11,32)	L	–	2
H. grandifolia Strandl. & L.O. Wms. (19,63)	L	–	2
H. quapara (Aubl.) Sprague (46)	L	–	1
Nyctaginaceae			
Pisonia aculeata L. (40)	L	–	1
Sapindaceae			
Paullinia fibrigera Radlk. (50)	L	–	1
P. glomerulosa Radlk. (13,56,64)	L	–	3
Serjania cornigera Turcz, (47)	L	–	1
S. mexicana (L.) Willd. (23)	L	–	1

$$P_x = 100[(L_{atm}/L_{pd}) - 1] \tag{3}$$

When L_{pd} was > L_{atm} (including situations where all the water from the manometer was absorbed by the shoot), the P_x was recorded as negative, but no attempt was made to quantify negative pressures because manometers are not able to accurately measure the negative pressures that can occur in plants. The bubble manometers gave P_x values near those recorded previously by electronic pressure transducers in a related study (Cochard et al. 1994) and were used because they cost much less for surveys involving many species.

Observations were made on at least three consecutive mornings at pre-dawn on all 65 individuals. Measurements were made on most species during the dry season and on at least one individual of every species during the wet season.

Following measurements of P_x the largest stem of each species was sampled and xylem vessel (or tracheid in the case of *L. venustrum*) diameters were measured as follows: The stem was cut transversely and the surface was shaved smooth with a fresh razor blade. Vessel diameter was measured as the radial width of vessel lumens, as seen in transverse view with a stereo microscope. All vessels within equidistant sectors of the transverse surface were sampled; each sector had vascular rays for marginal boundaries, and the pith and (outer) phloem as inner and outer boundaries. Radial vessel lumen diameters were measured with a camera lucida device and a digitizer and sample size was at least 100 vessels per stem. Vessels less than 25 µm in diameter were omitted from the sampling since the methods used did not allow for accurate detection of the narrowest vessels within a stem, and since the contribution of such narrow vessels to axial conductivity is minuscule when much larger vessels are present in a stem (Ewers and Fisher 1989; Ewers et al. 1991; Hargrave et al. 1994).

For species with positive P_x values, mean vessel diameter was used to calculate P_c based on Eq. 1. Since the xylem pressure measurements were not made exactly at soil level, as might be assumed for P_{xb} in Eq. 2, for the h_c values in Table 2, the height above soil level at which the measurement was made was added to the h_c calculated from Eq. 2.

Results

Of the 29 species of dicotyledons from ten families, only 3 species, all of the Dilleniaceae family, exhibited positive pre-dawn P_x. These were the large lianas *Doliocarpus major*, *Tetracera hydrophila*, and *T. portabellensis* (Tables 1,2). The highest P_x measured amongst the dicotyledons was 64 kPa, measured during the wet season on *D. major*, *T. hydrophila* had P_x values of 16 kPa both during the wet and dry season.

Of the three climbers that were non-dicotyledons, two had positive P_x values. The climbing fern (*Lygodium venustrum*), with twining leaves climbing to 3 m, had P_x values of 66 kPa near the base of the stipe (petiole). The viny bamboo (*Rhipidocladum racemiflorum*) climbed to the height of 4.5 m and had predawn P_x values of up to 120 kPa (Table 2). In contrast, the "semi-woody" monocotyledonous climber (*Smilax panamensis*) had negative P_x values at predawn, even during the wet season.

L. venustrum had tracheids up to 122 µm in diameter in the stipe, with a mean diameter of 64 µm (Table 2). All the other climbing species in the study had vessels in their xylem, with an overall mean (mean of the species means) of 150 µm (SD = 47), and an average maximum vessel diameter of 301 µm (SD = 118).

In *L. venustrum* and *R. racemiflorum* the h_c for vessel refilling far exceeded the maximum height of the specimen. In contrast, in the three lianas of the Dilleniaceae with positive P_x values, the h_c for vessel refilling was far less than the height of the specimens (Table 2).

Discussion

The best documented study of the vulnerability of a vine to embolism is for *Vitis vinifera* (Salleo and LoGullo 1989), which exhibited severe embolism at water potentials below −1.7 MPa. In contrast, in the vine-like bamboo *Rhipidocladum racemiflorum*, water potentials below −4.5 MPa were required to induce 50% loss of hydraulic conductance due to embolism. Thus there is reason to expect that different climbing plants differ considerably in their vulnerability to embolism.

At least for larger individuals, results of the present study do not support the hypothesis by Putz (1983) that tropical lianas might have sufficient root pressures to dissolve emboli in their stem xylem. A root pressure mechanism to remove embolism in stems might be most effective with either (1) deciduous plants, because the leafless condition would minimize transpiration or (2) smaller plants, because root pressure could reach the shoot tips with less pressure to overcome gravity. None of the observed vines in the present study were deciduous, even in the dry season, but the size of the mature plants and thus the possibilities for vessel refilling in the upper stems, did differ considerably between species.

Within the Dilleniaceae, the root pressures may be important in refilling vessels in the roots and in the lower stems. Our data for *Tetracera* are similar to results of Scholander et al. (1957) for this genus at the same site, where they found xylem pressures of 10–80 kPa. However, as noted by Scholander et al. (1957), the P_x values need to be considered in the context of the height of the plants. Our measured values of P_x near the base of the stems of Dilleniaceae (a maximum of 64 kPa in *Doliocarpus major*) was modest considering that those plants reached the canopy height of 18 m. Based on the above argument and our data, we conclude that the P_{xb} of 64 kPa would be adequate, given enough time, to refill embolized vessels of the roots and lower stems, at a

Table 2 Species with positive xylem pressures: maximum predawn xylem pressure (P_x) at h = 0.5 m, vessel diameter, critical pressure (P_c) for vessel refilling, critical height (h_c) for vessel refilling under static equilibrium conditions, and the maximum specimen height (h_s). Thirty-two species of climbing plants were sampled on Barro Colorado Island, Panama, (Table 1) but data are not shown for the 27 species with strictly negative pre-dawn P_x values

		Diameter				
	P_x (kPa)	Mean	SD (µm)	P_c (kPa)	h_c (m)	h_s (m)
Dilleniaceae						
Diliocarpus major	64	149	56	−1.9	7.1	18.0
Tetracera hydrophilia	16	196	80	−1.4	2.2	18.0
T. portobellensis	57	263	100	−1.1	6.3	18.0
Poaceae						
Rhipidocladum racemiflorum	120	196	56	−1.4	12.6	4.5
Schizaeaceae						
Lygodium venustrum	66	64^a	21	−4.4	7.5	3.0

[a] Tracheid, rather than vessel diameter

maximum height of just 7.1 m. However, the maximum theoretical heights for vessel refillings (h_c) that we calculated are overestimates of the likely maximum heights for vessel refilling, since they assumed no water flow and no leakage. In any event, the root pressure would not be adequate to refill vessels in the upper parts of the stems of the large lianas that we studied. The vast majority of the dicot vines lacked positive P_x even near the base.

Although there was anecdotal evidence that many tropical lianas had positive root pressures (Putz 1983; Ewers et al. 1991), prior to the present study and another study currently in press (Fisher et al. in press) there were few measurements to support this. In Fisher et al. (in press), predawn root pressures were identified in 61 of 109 species of tropical vines and woody species. That report suggested a much higher percentage of species with positive xylem pressures than in the present study. However, Fisher et al. (in press) included more herbaceous vines and more monocotyledonous climbers than in the present study. In addition, in Fisher et al. (in press), those species exhibiting predawn guttation from leaves were among the plants especially selected for study. In the present study all the lianas at a particular site were used, with no consideration of whether guttation occurred. Taken together, these studies imply that root pressures are less common in lianas than in more herbaceous climbers, and that certain families may have a strong tendency for root pressures, including the monocotyledonous family Araceae (10 of 10 species; Fisher et al. in press) and the dicotyledonous families Vitaceae (10 of 10 species; Fisher et al. in press) and Dilleniaceae (3 of 5 species, present study).

The only clear case of embolism repair via root pressures in a dicotyledonous liana is in temperate species of *Vitis*. This occurs when the plant is in a leafless condition with minimum transpiration. The first published report of root pressures in this genus may be by Hales (1727). More recent studies indicate that in the early spring the vessels are initially so dry that the displacement of air by water is accomplished by pushing air across dry pit membranes at leaf scars. After about half the vessels are refilled, further displacement of bubbles is by dissolution since many pit membranes become wet and the water menisci prevent bulk passage of air (Sperry et al. 1987).

In contrast to dicotyledonous lianas in the present study, the climbing fern *L. venustrum* and the viny bamboo *R. racemiflorum* exhibited root pressures that might be adequate to refill embolized vessels throughout the entire plant. *L. venustrum* had leaves that climbed to 3 m and P_{xb} values up to 66 kPa. The h_c was 7.5 m, suggesting that xylem pressures might be quite adequate for refilling of the tracheids even in the upper parts of the leaves. *Rhipidocladum racemiflorum* climbed to only 4.5 m but it had P_{xb} values up to 120 kPa and an h_c of 12.6 m. Furthermore, we found positive P_x values even at the most distal part of the stems in this species (Cochard et al. 1994), suggesting that root pressures could serve to refill embolized vessels throughout the shoot.

Davis (1961) reported positive root pressures in ten species of palm trees and in banana, *Musa sapientum*, but a lack of root pressure in five dicotyledonas trees and in a cycad. It was suggested that monocotyledons, and other taxa that lack secondary growth for the production of new vascular tissue in their stems, may often depend on root pressures for water transport. We now know that root pressures are not directly important for the high volume day-time transpiration in vascular plants, as was implied by Davis (1961) for monocotyledons. However, root pressure could be important for removing embolisms and thus maintaining hydraulic continuity in some plants lacking secondary growth. In addition to palm trees, strong root pressures have also been reported for other moncots such as sugar cane (Meinzer et al. 1992), bamboos (Cochard et al. 1994) and hemiepiphytic aroids (Fisher et al. in press), as well as in some ferns (Sperry 1983; Fisher et al. in press). Similarly, the two species in the present study that produced positive pressures that could be adequate to refill vessels in their upper stems and leaves, *R. racemiflorum* and *L. venustrum*, both lack secondary growth. In contrast, dicotyledons have the ability to produce new secondary xylem in their axes, which is another mechanism to enhance conductivity following embolism (Zimmermann and Brown 1971; Kolb and Davis 1994).

Although root pressures can be eliminated as a mechanism for embolism reversal in most of the studied plants, root pressures may not be the only mechanism by which embolisms can be reversed in the xylem. A recent study indicates that in the evergreen shrub *Laurus nobilis* xylem embolism can be reversed in the absence of positive root pressures, even at xylem water potentials of −30 kPa (Salleo et al. 1996). For that species phloem transport appears to be essential to the refilling process, although the exact mechanism of refilling is unknown. Also unknown is the mechanism by which conifer tracheids can often reverse embolism even when the xylem appears to be under negative pressure (Borghetti et al. 1991; Grace 1993; Edwards et al. 1994). In contrast to embolism reversal studies, several seasonal studies of embolism in woody angiosperms suggest that in some species once embolism occurs in vessels, it will result in permanent blockage, with new wood production as the only mechanism to enhance conductivity (Sperry and Sullivan 1992; Cochard and Tyree 1994; Kolb and Davis 1994; Sperry et al. 1994).

In terms of global distribution, there is a strong inverse correlation between latitude and liana abundance. The inverse correlation with latitude holds true whether one considers the number of liana species per hectare, the number of liana stems per hectare, or the percentage of liana species in the flora (Gentry 1991). The wide vessels of climbing plants in the present study (the overall mean was 150 μm, versus 94 μm for dicotyledous plants as a whole, according to Metcalfe and Chalk 1950) were much as expected. Wide vessels appear to be an integral part of the water relations/resource allocation "strategy" of lianas (Ewers et al. 1991; Ewers and

Fisher 1991). While resistance to drought-induced embolism is very weakly correlated with vessel or tracheid diameter, resistance to permanent, freezing-induced embolism is strongly correlated to diameter of the vessel or tracheid (Cochard and Tyree 1990; Sperry et al. 1994; Tyree et al. 1994a). Considering that wide vessels are quite prone to freezing-induced embolism and that most large lianas appear to lack positive root pressures sufficient for embolism reversal in their shoots, freezing-induced embolism could be a factor that helps to limit the global distribution of climbing plants. However, this hypothesis is tenuous until more is learned about the vulnerability of lianas to embolism and about the possibility of embolism reversal by means other than root pressure.

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