

Hydraulic conductivity and embolism in the mangrove tree *Laguncularia racemosa*

FRANK W. EWERS,^{1,2} JÓRGE LOPEZ-PORTILLO,³ GUILLERMO ANGELES³ and
JACK B. FISHER⁴

¹ Department of Plant Biology, Michigan State University, East Lansing, MI 48824-1312, USA

² Corresponding author (ewers@msu.edu)

³ Instituto de Ecología, A.C., Apdo Postal 63, Xalapa 91070 Veracruz, México

⁴ Fairchild Tropical Garden, 11935 Old Cutler Road, Miami, FL 33156, USA

Received January 22, 2003; accepted February 8, 2004; published online July 1, 2004

Summary We measured xylem pressure potentials, soil osmotic potentials, hydraulic conductivity and percent loss of conductivity (PLC) due to embolism, and made microscopic observations of perfused dye in the white mangrove tree, *Laguncularia racemosa* (L.) Gaertn. f., (1) to determine its vulnerability to air embolism compared with published results for the highly salt-tolerant red mangrove tree, *Rhizophora mangle* L., and (2) to identify possible relationships between air embolism, permanent blockage of vessels and stem diameter. *Laguncularia racemosa* was more vulnerable to embolism than reported for *R. mangle*, with 50 PLC at -3.4 MPa. Narrow stems (5-mm diameter) had higher PLC than larger stems (8.4- or 14-mm diameter) of the same plants. Basic fuchsin dye indicated that up to 89% of the vessels, especially in the narrow stems, had permanent blockage that could not be reversed by high pressure perfusion. Air embolism could lead to permanent vessel blockage and eventual stem mortality. Such vulnerability to embolism may restrict the growth of *L. racemosa* and limit its distribution to less salty areas of mangrove communities.

Keywords: differential mortality of stems, nonconductive xylem, specific conductivity, vulnerability curve, white mangrove.

Introduction

Mangrove trees have long been recognized for their ability to filter and desalinate water as it enters the roots (Scholander et al. 1968), to tolerate low pressure potentials in the xylem (Scholander et al. 1962, 1965b), and to resist cavitation of water columns in the xylem despite low xylem pressure potentials (Sperry et al. 1988b). Also well known in mangrove communities is the banded pattern of zonation, with different species occurring in bands parallel to the shore. This pattern is often attributed to gradients in substrate salinity (Mizrachi et al. 1980, Ball 2002).

The best studied mangrove species in terms of xylem trans-

port is the red mangrove, *Rhizophora mangle* L. (Sperry et al. 1988b, Zimmermann et al. 1994, Becker et al. 1997, Sobrado 2000, Melcher et al. 2001). Based on xylem water potentials measured in the field and its distribution within the mangrove community, the white mangrove, *Laguncularia racemosa* (L.) Gaertn. f., is less tolerant of salinity than the red mangrove (Tomlinson 1986, Sternberg et al. 1991, Medina and Francisco 1997). We hypothesized that *L. racemosa* resists water stress-induced embolism less than has been reported in the literature for *R. mangle*.

There is some evidence that embolism can lead to die-off of the smaller branches of drought-stressed trees and shrubs, while larger branches persist (Tyree et al. 1994, Rood et al. 2000, Davis et al. 2002). The narrow, more distal twigs experience lower potentials than the older, larger diameter stems, as a result of their position in the water potential gradient through the plant, but the possible impact of greater xylem tension on water transport is difficult to assess in the absence of a reliable measurement of embolism. The conductivity method (Sperry et al. 1988a), which has been widely used to measure percent loss of conductivity (PLC) due to embolism, assumes that dysfunction as a result of embolism can be experimentally reversed by high pressure perfusion. However, the conductivity method ignores vessels in which blockage is not reversed by high pressure perfusion. In the present study, in addition to measuring PLC, we perfused dyes into experimental and control stems and then made microscopic counts of vessels that were conductive before and after high pressure perfusion. With this experimental system we were able to explore the possible scenario of air embolism, measured as PLC, leading to permanent blockage, identified by the lack of dye perfusion. In addition to identifying permanent blockage, the dye quantified anatomical embolism (AE), that is, air embolism measured with the use of dye, for comparisons with PLC. Comparisons of the native embolism in narrow, medium and wide stems were also made. We then dehydrated stems in the laboratory to determine whether narrow stems were inherently more vulnerable to embolism than wider stems.

Materials and methods

Study site

Trees of *L. racemosa* were sampled from a mixed *Laguncularia racemosa*–*Avicennia germinans* stand at the northwest limit of the La Mancha Lagoon in the State of Veracruz, Mexico (96°22' W, 19°35' N). Mean annual precipitation at the site is 1200 mm.

Osmotic and pressure potentials

Twig xylem pressure potentials were measured with a pressure chamber (Scholander et al. 1965a). Osmotic potentials of the soil samples, the tap water at the field station, and the xylem sap extracted from twigs with a pressure chamber were measured with a psychrometer (Wescor C-52 sample chambers and an HR-33T Dew Point Microvoltmeter, Wescor, Logan, UT). Osmotic and pressure potentials were measured in the wet season as well as on May 16, 2002, at the peak of the dry season, to determine the lowest (most negative) osmotic and pressure potentials that the trees might experience at the site. Soil was sampled at a depth of 10 to 15 cm, where feeder root density was greatest at this site (Angeles et al. 2002).

Hydraulic conductivity and PLC due to embolism

In a preliminary experiment, 20 stems greater than 3 m in length were sampled to determine maximum vessel length by the air method (Greenidge 1952, Zimmermann and Jeje 1981). It was found that maximum vessel lengths were between 0.97 and 2.0 m. Therefore, to minimize the introduction of new embolisms, only stems greater than 2.0 m in length were sampled for measurements of hydraulic conductivity and embolism.

An embolism vulnerability curve was derived by the dehydration conductivity method (Sperry et al. 1988a). We used vertical stems of *L. racemosa* obtained from mature 6-m-tall trees. To obtain a broad sample of the population, we sampled one medium-diameter stem segment (about 8.5 mm diameter) from each of 68 individuals during the rainy season (August 1999), when native embolism should have been minimal.

Shoots cut from 68 plants in the field were either bagged immediately, or taken to the laboratory and allowed to dehydrate for various lengths of time before being bagged overnight to allow for equilibration of water potentials. After 12 h of equilibration, a twig was sampled from each shoot for determination of xylem pressure potential by the pressure chamber method (Scholander et al. 1965a). Stems were repeatedly recut under water to produce 10-cm-long segments with a diameter of about 8.5 mm. The PLC of these segments was calculated from the hydraulic conductance per pressure gradient (conductivity or k_h) measured before (initial k_h) and after removing embolisms by high pressure perfusion at 100 kPa. The high pressure perfusion was repeated until a maximum k_h value was obtained (Sperry et al. 1988a).

Tap water was run through a 0.2- μ m in-line filter for measurements of k_h and PLC. The tap water used at the field station was fairly saline; we measured the osmotic potential as -0.30 MPa ($n = 5$, $SE = 0.012$), corresponding to an osmolarity of 124 mmol. The osmotic potential of the xylem sap extracted from five twigs with a pressure chamber was -0.45 MPa

($SE = 0.047$), similar to the osmotic potential of the tap water we used for conductivity measurements. In preliminary experiments, we found no significant difference in k_h and PLC for measurements made using filtered tap water versus a filtered solution of 15 mM ascorbic acid in deionized water. Therefore, we concluded that filtered tap water at the research station was an appropriate solution for making the measurements of k_h and PLC, and that a hydrogel effect (Zwieniecki et al. 2001) would not influence the results such as might happen if pure deionized water was perfused through the stems.

We plotted PLC as a function of xylem pressure potential, and applied the exponential sigmoidal equation to determine the water potential corresponding to 50 PLC, as described by Pammenter and Vander Willigen (1998). Xylem specific conductivity (k_s) was calculated as k_h divided by the xylem transverse area at the midpoint of the stem segment (Tyree and Ewers 1991).

Stem diameter and embolism

Comparisons were made between wide, medium and narrow stems at two xylem water potentials, to determine the possible interactive effects of stem diameter and water-stress-induced embolism. For these experiments, a stem segment of large diameter (wide stem, about 14 mm diameter) and another, more distal stem of smaller diameter (narrow stem, about 5 mm diameter) on the same shoot were measured and compared for conductivity and PLC. In one treatment, designed to show native PLC, the shoots were bagged in the field and equilibrated to xylem water potentials ranging from -1.2 to -1.6 MPa. In another treatment, the shoots were dehydrated in the laboratory before being bagged for overnight equilibration to -2.5 to -3.3 MPa. Values of PLC corresponding to water potential ranges of -1.2 to -1.6 MPa and -2.5 to -3.3 MPa attained by the medium-diameter stems during the vulnerability curve determination were compared with those of wide and narrow stems subjected to the same ranges of water potential.

Anatomical observations versus PLC

To determine the anatomical basis for PLC, two adjacent stem segments on each of 17 shoots were selected for dye perfusion. Of the two segments, one was randomly selected as the control; i.e., air embolisms were not removed by high pressure perfusion prior to perfusion with dye. The other segment was perfused with dye after final measurements of maximum conductivity were made. For dye perfusion, each stem segment was attached to a Tygon tube filled to the top with filtered 1.0% basic fuchsin dye solution. The stem segment was kept in a horizontal position and the tube was bent vertically to create a pressure head of 15 cm. After 30 min of perfusion, the dye was replaced with water and the stems were perfused for an additional hour. The stem segments were then detached from the tube and allowed to air-dry overnight. The stem segments were cut 3 cm from the perfusion port, and the exposed transverse surface was shaved smooth with a razor blade. The stained and unstained vessels at that position were counted with the aid of a dissecting microscope. For representative sampling, the stem cross-sectional area was subdivided into 4, 8, or 16 sectors by radial lines cut with a razor into the transverse surface. Equally

spaced sectors were used for vessel counting and all the stained and unstained vessels in two or four sectors per stem were counted. Unstained vessels in the experimental stems were regarded as irreversibly embolized.

Preliminary results showed a high percentage of stained vessels, up to 89%, even in the experimental stems. To test whether staining of vessels could be related to PLC by accounting for permanently nonconductive vessels, anatomical embolism (AE) was calculated as: AE = % stained vessels experimental – % stained vessels control.

Unlike AE, which counts the number of vessels, the PLC measurement is weighted toward wider vessels. According to Poiseuille's law, wider vessels will contribute a much greater portion to the total conductivity. The measurements of AE should have been equal to PLC assuming either that the different vessels in a stem were equally conductive (a bad assumption), or that different diameter vessels in a stem segment were equally prone to embolism, which is contrary to what is known to happen in some plants (Salleo and Lo Gullo 1986, Cochard and Tyree 1990, Hargrave et al. 1994, Davis et al. 1999).

Vessel diameters versus stem diameter

Because the results indicated that wide stems had both lower PLC values and a lower percentage of irreversible embolism than narrow stems, and because there are some reports of wide vessels in a plant being more prone to water-stress-induced embolism than narrow vessels, we sought to determine the relationship between stem diameter and xylem vessel diameter in this species. Stem segments of approximate diameters 4, 6, 8, 10, 12 and 14 mm were sampled from each of nine trees, for a total sample size of 54 stem segments.

Transverse sections were made with a sliding microtome at 50–60 μm, stained with 0.1% aqueous safranin O and all the vessels within randomly selected fields of view were measured in digitized images viewed through a compound microscope. We sampled at least four fields of view for narrow stems (4–6 mm) and up to nine fields of view for wider stems. The vessel hydraulic mean diameter for a stem segment was calculated as the summation of the fifth power of vessel diameters divided by the summation of the fourth power of vessel diameters (Sperry et al. 1994, Davis et al. 1999).

Results

Pressure potentials, PLC and stem diameter

The embolism vulnerability curve, constructed from data ob-

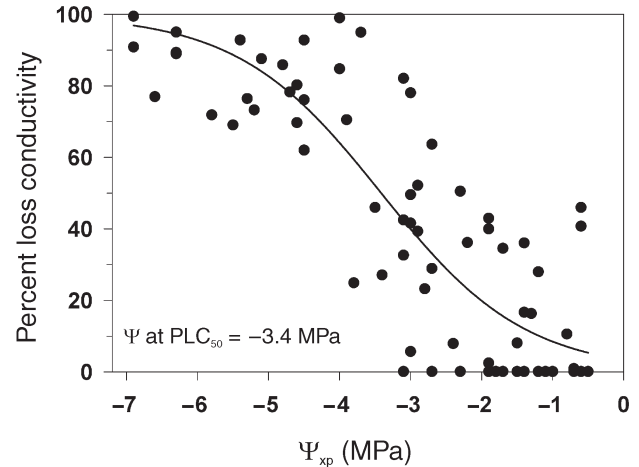


Figure 1. Percent loss of conductivity due to embolism as a function of xylem pressure potential (Ψ_{xp}) in medium-diameter stems. Each value is from one individual. The curve fit was exponential sigmoidal (Pammenter and Vander Willigen 1998).

tained by the dehydration conductivity method, is shown in Figure 1. Based on the Pammenter and Vander Willigen (1998) coefficient for dealing with a sigmoid curve, the statistical 50% loss in conductivity due to embolism occurred at –3.4 MPa (Figure 1). The fit accounts for 74% of the total variability in the data and is significant at $P < 0.001$. The PLC typically approached 75 to 100% at water potentials below –4.0 MPa. The vulnerability curve was based entirely on medium-diameter stems, ranging from 7 to 11 mm in diameter.

Comparisons of wide, medium and narrow stems at two xylem pressure potentials indicated interactive effects of stem diameter, conductivity and PLC. Wide stems had significantly greater k_h and k_s values than narrow stems, with medium-diameter stems having intermediate values (Table 1). The narrow stems had significantly greater PLC than the medium and wide stems when the shoots were kept at –1.2 to –1.6 MPa, indicating that native embolism was greatest in narrow stems. When shoots were dehydrated in the laboratory to reach equilibrated xylem water potentials of –2.5 to –3.3 MPa, the three stem diameter classes each showed significant increases in PLC, but PLC did not differ significantly between diameter classes (Figure 2).

Microscopic observations, PLC and irreversible embolism

The combined vessel staining and conductivity experiments showed a strong correlation between PLC and AE (Figure 3).

Table 1. Means (SE) of stem diameter, hydraulic conductivity (k_h) and specific conductivity (k_s) in narrow, medium and wide stems of *Laguncularia racemosa*. The F -values and coefficients of determination were obtained by one-way ANOVA ($n = 19$ for each stem size). Within a row, similar letters indicate no significant differences (Tukey-Kramer HSD multiple comparisons for one-way ANOVA) and *** = $P < 0.0001$.

	Narrow	Medium	Wide	F	r^2
Stem diameter (mm)	4.8 (0.3) a	8.4 (0.3) b	13.9 (0.3) c	268 ***	0.91
$k_h \times 10^{-5}$ (kg m MPa ⁻¹ s ⁻¹)	2.3 (3.0) a	14 (3.0) b	47 (3.0) c	78.5 ***	0.73
k_s (kg MPa ⁻¹ s ⁻¹ m ⁻¹)	1.23 (0.22) a	2.38 (0.22) b	3.13 (0.22) b	18.2 ***	0.38

The anatomical measurement (AE) of reversible embolism appeared to measure the same characteristic as the physiological measurement (PLC). This was consistent with vessels differing in diameter being equally prone to embolism; otherwise the relationship between AE and PLC should not have been linear.

The percentage of vessels that were permanently embolized, as indicated by the absence of stain even after high pressure perfusion, was positively correlated with PLC (Figure 4a), consistent with potentially reversible embolism eventually resulting in permanent blockage.

Irreversible embolism was inversely correlated with stem diameter; i.e., a greater percentage of permanently blocked vessels occurred in narrow stems than in wide stems (Figure 4b). Irreversible embolism ranged from a low of 8% in the wider stems to a high of 89% in narrow stems. Thus, narrow stems tended to have greater PLC as well as greater permanent blockage of vessels.

Vessel hydraulic mean diameter was positively correlated with stem diameter (Figure 5). There was a similar positive correlation between stem diameter and both mean and maximum vessel diameter (data not shown), indicating that, as stems increased in diameter, they produced wider vessels.

Osmotic and pressure potentials

The most hydrated shoots that we sampled were collected before dawn during a rainstorm on August 19, 1999. The 10 shoots were bagged immediately in the field and had equilibrated xylem pressure potentials of -0.69 MPa (SE = 0.058). At the other extreme, during the peak of the dry season (May 2002), mean midday xylem pressure potential was -2.62 MPa (SE = 0.16) for twigs, whereas soil osmotic potential was -0.82 MPa (SE = 0.38).

Discussion

As we hypothesized, *L. racemosa* was considerably more vulnerable to water stress-induced embolism than the more salt-

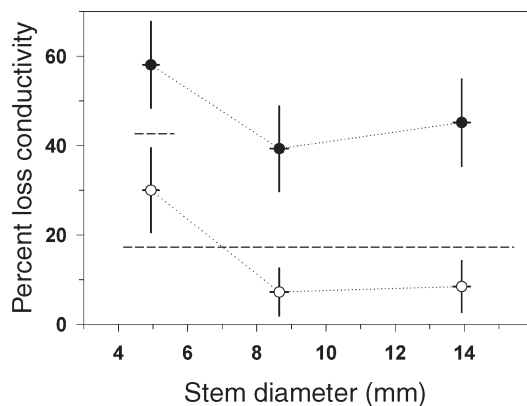


Figure 2. Percent loss of conductivity (\pm SE) for narrow, medium and wide stems at two water potentials. Symbols: \circ = stems at -1.2 to -1.6 MPa, without dehydration treatment; and \bullet = shoots dehydrated to -2.5 to -3.3 MPa. Horizontal dashed lines separate values that are significantly different at $P < 0.001$.

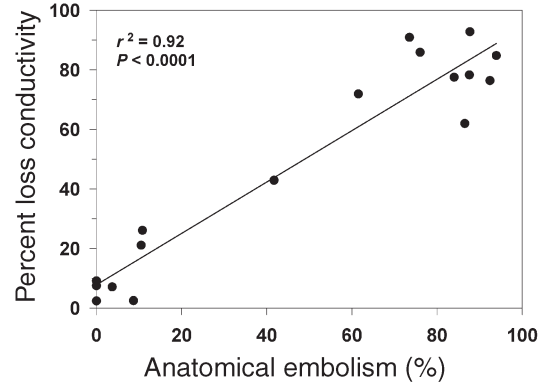


Figure 3. Percent loss of conductivity as a function of anatomical embolism. The slope of the linear regression line was not significantly different from a 1:1 relationship. Each value is from one individual.

tolerant species *R. mangle*. In our study, *L. racemosa* became 50% embolized at a xylem pressure potential of -3.4 MPa, whereas similar diameter stems of *R. mangle* became 50% embolized at about -6.3 MPa (Sperry et al. 1988b). Melcher et al. (2001) found that, at coastal sites where soil water potential was -2.6 MPa, *R. mangle* plants became 50% embolized at -6.3 MPa, as found by Sperry et al. (1988b), whereas plants growing at an estuarine site, where soil water potential was -0.4 MPa, became 50% embolized at -4.4 MPa, which is closer to, but still more negative than the value of -3.4 MPa

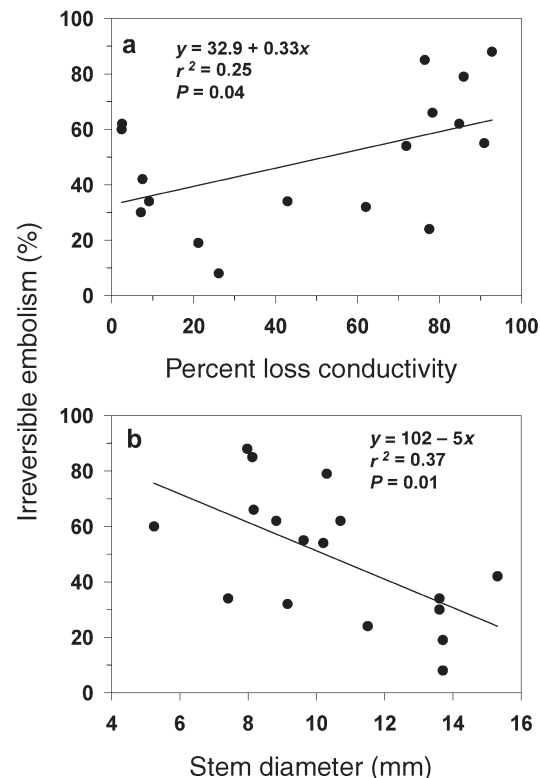


Figure 4. Percent irreversible embolism as functions of (a) percent loss conductivity and (b) stem diameter. Each value is from one individual.

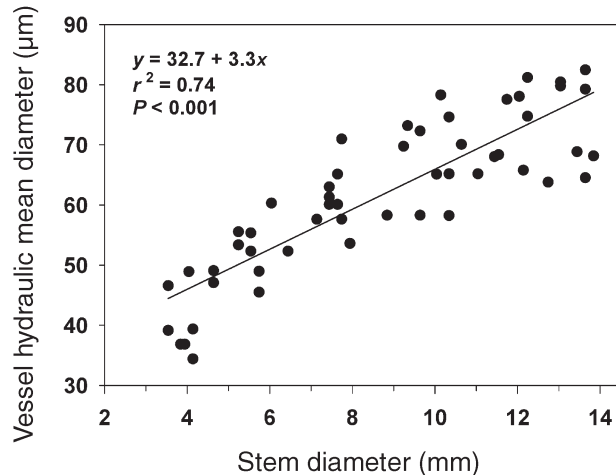


Figure 5. Vessel hydraulic mean diameter (Σ vessel diameter⁵/ Σ vessel diameter⁴) as a function of stem diameter. The regression is a linear fit, and each value is from one stem segment.

that we found for *L. racemosa*. Our results are consistent with xylem embolism limiting the distribution of *L. racemosa* to less saline sites in the mangrove ecosystem, but we did not examine possible phenotypic nor ecotypic variation in plants.

Compared with previous reports for similar diameter stems of *R. mangle*, *L. racemosa* stems had higher maximum k_s values. For medium diameter stems, we found a mean maximum k_s (\pm SE) of $2.4 \pm 0.1 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ for *L. racemosa* versus $1.9 \pm 0.1 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ reported for *R. mangle* (Sperry et al. 1988b). Melcher et al. (2001) reported even lower k_s values for *R. mangle*, $1.4 \pm 0.2 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ at estuarine sites and still lower values of $0.4 \pm 0.1 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ at a coastal site. In the study by Sobrado (2000), the trends were similar, but narrow 2- to 3-mm-diameter stems were used, and the k_s values were two orders of magnitude lower than in our study. In that study, the stems of *L. racemosa* had 3.7 times greater k_s values than *R. mangle*.

However, the greater hydraulic efficiency of *L. racemosa* relative to *R. mangle* might be reversed in more saline soils, as a result of water-stress-induced embolism. The *L. racemosa* stems that we examined would appear to be at risk for runaway embolism and death of shoots or of the entire plant, especially when xylem pressure potentials fall below -4.0 MPa .

When interpreting the vulnerability curve, which was constructed during the wet season, it should be noted that, during the dry season, the twigs experienced xylem pressure potentials of about -2.6 MPa . Thus the embolism that occurred in some stems at xylem pressure potentials less negative than this value may have been irreversible native embolism caused by water stress experienced during the previous dry season.

The positive correlation between stem diameter and mean vessel hydraulic diameter that we found for *L. racemosa* is typical for plants in general (Zimmermann 1983, Tyree and Zimmermann 2002). It would explain why the wider stems tended to have greater k_h and k_s values than narrow stems, but it would not explain why wider stems tended to have lower embolism and less permanent blockage. This finding is in con-

trast to the trend reported in the literature (Salleo and Lo Gullo 1986, Cochard and Tyree 1990, Hargrave et al. 1994, Sperry et al. 1994, Davis et al. 1999), that wider vessels are more prone to dysfunction. For *L. racemosa*, other factors, such as position within the plant, may be more important than vessel diameter in determining vessel dysfunction.

Although narrow, more distal stems of *L. racemosa* tended to be more embolized than wider, more proximal stems, dehydration in the laboratory induced similar increases in embolism for wide, medium and narrow stems. However, laboratory dehydration does not necessarily simulate the conditions that stems may experience over the course of a dry season on intact plants.

In water-stressed plants of *Ceanothus crassifolius* Torr. in the field, once leaves showed discoloration, the twigs were 100% embolized and starting to die off (Davis et al. 2002). Similarly, in *Populus deltoides* Bartr. ex. Marsh., shoots with premature leaf senescence tended to have higher embolism and were much more likely to die the next season than shoots with green foliage (Tyree et al. 1994, Rood et al. 2000). All of the stems that we selected for measurements of hydraulic conductivity and embolism were healthy in appearance, but some may have had a history of exposure to low water potentials during past dry seasons. Narrow stems inherently have less redundancy in their vascular system, and so embolism events may be accentuated for particular twigs on intact plants, for instance, those with the most severe exposure to high light, high temperature, or salt spray.

The average stem embolism does not represent what happens to individual stems. The "average stem" will die off before becoming a large stem, and embolism could be a factor determining stem survival, consistent with the inverse correlation between stem diameter and percent irreversible embolism, and the positive correlation between PLC and irreversible embolism. Only a few stems survive to become wide stems, and the survivors may be the ones with the lowest embolism.

The PLC due to embolism is a measure of the embolism that is reversible experimentally by perfusing the stems with degassed solution at high pressure. After a vessel becomes embolized, it may develop tyloses and gums that fill its lumen, or special incrustations at the pit membrane, all of which can result in the vessel becoming permanently nonconductive (Kinimouth 1972, Wheeler 1982, 1983, Zimmermann 1983, Cochard and Tyree 1990). Even in apparently healthy shoots, we found that up to 89% of the vessels had irreversible blockage. Such blockage can be easily overlooked in measurements of PLC, the typical method of measuring embolism. Perhaps a similar blockage occurs in xylem of *R. mangle*, for which Zimmermann et al. (1994) reported that a high percentage of the vessels contained high molecular weight organic compounds (mucilage). The mucilage might play a role in long-distance transport or embolism reversal, but an alternate interpretation would be that all of the mucilage containing vessels were nonconductive and only the vessels lacking mucilage were conductive.

To conclude, embolism and permanent blockage of vessels

may limit the growth and distribution of species in the mangrove habitat, but phenotypic versus genetic factors need to be elucidated to understand the ecology and evolution of the banded pattern of distribution characteristic of mangrove communities. A demographic approach to studying reversible air embolism and permanent blockage, with as much emphasis on the variation in results as on average results, may be helpful in exploring stem and plant mortality in extreme environments.

References

- Angeles, G., J. Lopez-Portillo and F. Ortega-Escalona. 2002. Functional anatomy of the secondary xylem of roots of the mangrove *Laguncularia racemosa* (L.) Gaertn. (Combretaceae). *Trees* 16: 338–345.
- Ball, M.C. 2002. Interactive effects of salinity and irradiance on growth: implications for mangrove forest structure along salinity gradients. *Trees* 16:126–139.
- Becker, P., A. Asmat, J. Mohamad, M. Moskin and M.T. Tyree. 1997. Sap flow rates of mangrove trees are not unusually low. *Trees* 11: 432–435.
- Cochard, H. and M.T. Tyree. 1990. Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiol.* 6:393–407.
- Davis, S.D., J.S. Sperry and U.G. Hacke. 1999. The relationship between xylem conduit diameter and cavitation caused by freezing. *Am. J. Bot.* 86:1367–1372.
- Davis, S.D., F.W. Ewers, J.S. Sperry, K.A. Portwood, M.C. Crocker and G.C. Adams. 2002. Shoot dieback during prolonged drought in *Ceanothus* (Rhamnaceae) chaparral of California: a possible case of hydraulic failure. *Am. J. Bot.* 89:820–828.
- Greenidge, K.N.H. 1952. An approach to the study of vessel length in hardwood species. *Am. J. Bot.* 39:570–574.
- Hargrave K.R., K.J. Kolb, F.W. Ewers and S.D. Davis. 1994. Conduit diameter and drought-induced embolism in *Salvia mellifera* Greene (Labiatae). *New Phytol.* 126:695–705.
- Kininmouth, J.A. 1972. Permeability and fine structure of certain hardwoods and effects on drying. II. Differences in fine structure of *Nothofagus fusca* sapwood and heartwood. *Holzforschung* 26: 32–38.
- Medina, E. and M. Francisco. 1997. Osmolarity and $\delta^{13}\text{C}$ of leaf tissues of mangrove species from environments of contrasting rainfall and salinity. *Estuar. Coast. Shelf Sci.* 45:355–361.
- Melcher, P.J., G. Goldstein, F.C. Meinzer, D.E. Yount, T.J. Jones, N.M. Holbrook and C.X. Huang. 2001. Water relations of coastal and estuarine *Rhizophora mangle*: xylem pressure potential and dynamics of embolism formation and repair. *Oecologia* 126: 182–192.
- Mizrachi, D., R. Pannier and F. Pannier. 1980. Assessment of salt resistance mechanisms as determinant physio-ecological parameters of zonal distribution of mangrove species. I. Effects of salinity stress on nitrogen metabolism balance and protein synthesis in the mangrove species *Rhizophora mangle* and *Avicennia nitida*. *Bot. Mar.* 23:289–296.
- Pamenter, N.W. and C. Vander Willigen. 1998. A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiol.* 18:589–593.
- Rood, S.B., S. Patino, K. Coombs and M.T. Tyree. 2000. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees* 14:248–257.
- Salleo, S. and M.A. Lo Gullo. 1986. Xylem cavitation in nodes and internodes of whole *Chorisia insignis* H.B. et K. plants subjected to water stress: relations between xylem conduit size and cavitation. *Ann. Bot.* 58:431–441.
- Scholander, P.F. 1968. How mangroves desalinate seawater. *Physiol. Plant.* 21:251–261.
- Scholander, P.F., H.T. Hammel, E.A. Hemmingsen and W. Garay. 1962. Salt balance in mangroves. *Plant Physiol.* 37:722–729.
- Scholander, P.F., H.T. Hammel, E.D. Bradstreet and E.A. Hemmingsen. 1965a. Sap pressure in vascular plants. *Science* 148:339–340.
- Scholander, P.F., H.T. Hammel, E.A. Hemmingsen and E.D. Bradstreet. 1965b. Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. *Proc. Natl. Acad. Sci. USA* 52:119–125.
- Sobrado, M.A. 2000. Relation of water transport to leaf gas exchange properties in three mangrove species. *Trees* 14:258–262.
- Sperry, J.S., J.R. Donnelly and M.T. Tyree. 1988a. A method for measuring hydraulic conductivity and embolism in the xylem. *Plant Cell Environ.* 11:35–40.
- Sperry, J.S., M.T. Tyree and J.R. Donnelly. 1988b. Vulnerability of xylem to embolism in a mangrove vs. an inland species of Rhizophoraceae. *Physiol. Plant.* 74:276–283.
- Sperry, J.S., K.L. Nichols, J.E.M. Sullivan and S.E. Eastlack. 1994. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. *Ecology* 75:1736–1752.
- Sternberg, L. da S.L., N. Ish-Shalom-Gordon, M. Ross and J. O'Brien. 1991. Water relations of coastal plant communities near the ocean/freshwater boundary. *Oecologia* 88:305–310.
- Tomlinson, P.B. 1986. The botany of mangroves. Cambridge University Press, Cambridge, 397 p.
- Tyree, M.T. and F.W. Ewers. 1991. The hydraulic architecture of trees and other woody plants. *New Phytol.* 119:345–360.
- Tyree, M.T. and M.H. Zimmermann. 2002. Xylem structure and the ascent of sap. 2nd Edn. Springer-Verlag, Berlin, 278 p.
- Tyree, M.T., K.J. Kolb, S.B. Rood and S. Patino. 1994. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta—possible factor in the decline of the ecosystem. *Tree Physiol.* 14: 455–466.
- Wheeler, E.A. 1982. Ultrastructural characteristics of red maple (*Acer rubrum* L.) wood. *Wood and Fiber* 14:43–53.
- Wheeler, E.A. 1983. Intervascular pit membranes in *Ulmus* and *Celtis* native to the United States. *Int. Assoc. Wood Anat. Bull. N.S.* 4: 79–88.
- Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin, 143 p.
- Zimmermann, M.H. and A.A. Jeje. 1981. Vessel-length distribution in stems of some American woody plants. *Can. J. Bot.* 59: 1882–1892.
- Zimmermann, U., J.J. Zhu, F.C. Meinzer et al. 1994. High molecular weight organic compounds in the xylem sap of mangroves: implications for long-distance water transport. *Bot. Acta* 107:218–229.
- Zwieniecki, M.A., P.J. Melcher and N.M. Holbrook. 2001. Hydrogel control of xylem hydraulic resistance in plants. *Science* 291: 1059–1062.