Whole-plant hydraulic resistance and vulnerability segmentation in *Acer saccharinum*

MAKOTO TSUDA[1,3] and MELVIN T. TYREE[1,2]

[1] *Department of Botany, University of Vermont, Burlington, VT 05405, USA*

[2] *USDA Forest Service, Northeastern Forest Experiment Station, P.O. Box 968, Burlington, VT 05402, USA*

[3] *Present address: Faculty of Bioresources, Mie University, Tsu 514, Japan*

Summary   Hydraulic properties were studied in *Acer saccharinum* L., a riparian species that also grows well on a dry soil when transplanted. Hydraulic resistances were measured by two independent techniques: a new high-pressure flowmeter (HPFM) method and a conventional evaporative flux (EF) method. Vulnerability to cavitation was also investigated on petioles, stems and roots using a hydraulic conductivity technique.

Vulnerability segmentation was found, i.e., roots, stems and petioles had different vulnerabilities to xylem dysfunction. Petioles were most vulnerable with 50% loss of hydraulic conductivity at −0.5 MPa, roots were least vulnerable (50% loss at −2.2 MPa) and stems were intermediate in vulnerability.

The HPFM and the EF methods gave comparable results, except that the EF method gave a significantly higher value for resistance across petioles plus leaves. Native embolism was high enough to explain the discrepancy in resistance across petioles plus leaves between the HPFM and the EF methods, indicating that the HPFM estimates the minimum (potential) hydraulic resistance of plants. Whole-plant hydraulic resistance of *A. saccharinum* was low compared to resistances of other temperate species.

The hydraulic characteristics of *A. saccharinum* were consistent with adaptation to its typical environment: low whole-plant resistance assures high transpiration rates in the presence of sufficient water, and vulnerability segmentation provides the ability to survive during droughts through shedding of expendable organs.

Keywords: cavitation, embolism, evaporative flux method, high-pressure flowmeter method, petioles, roots, stems.

Introduction

Since the pioneering work of Zimmermann (1978), hydraulic architectures have been extensively assessed and discussed in terms of the evolution and adaptation of plants to various environments (e.g., Tyree and Ewers 1991, Tyree et al. 1994*a*). Quantitative studies on whole-shoot hydraulic architecture and its relation to evaporative flux have been conducted with the aid of models (Edwards et al. 1986, Tyree 1988, Tyree and Sperry 1988) and by measuring resistances of excised shoots (Hellkvist et al. 1974, Roberts 1977, Tyree et al. 1993*a*, 1993*b*, Yang and Tyree 1993, 1994). Root resistances, R_{root}, have been much less studied. Some studies have generalized that the root resistance to water flow through whole plants is greater than the shoot resistance (e.g., Kramer 1983, Boyer 1985), but reported R_{root} values vary, ranging from 20 to 90% of whole-plant resistance, R_{plant} (e.g., Hellkvist et al. 1974, Roberts 1977, Rieger 1989). Because R_{plant} depends greatly on R_{root}, the scarcity of values of R_{root} reduces our quantitative understanding of hydraulic architecture of whole plants.

The conventional method of measuring plant resistance, which we call the evaporative flux, EF, method, involves the measurement of steady-state evaporative flux densities from leaves and leaf to soil water potential gradients. Values of R_{plant} and the component resistances of the shoot are calculated from water potential differences between each plant part during steady-state water flow (e.g., Hellkvist et al. 1974, Roberts 1977, Running 1980). Recently, Tyree et al. (1994*c*, 1995) reported novel methods of measuring R_{root} using a high-pressure flow meter, HPFM, that is independent of the EF method. The HPFM method measures shoot resistance, R_{shoot}, as well as R_{root}, so R_{plant} (i.e., $R_{shoot} + R_{root}$) can be obtained. Although pressure chambers have been used to obtain pressure-driven root and stem (i.e., shoots less leaves) resistances (Rieger 1989), the HPFM method differs from the EF method in several important ways. It is much faster; it allows rapid determination of linearity between pressure and flow (see below); it measures root resistance while water flows opposite to the normal direction; and it permits determination of whole-shoot resistances (stems plus leaves). So far, we know of no studies in which the EF and HPFM methods have been compared.

The vulnerability of xylem to cavitation may change the efficiency of the hydraulic architecture because cavitation increases the hydraulic resistance of xylem (Tyree and Sperry 1989, Sperry and Pockman 1993). Xylem vulnerability differs widely among species (cf. Tyree et al. 1994*a*). It also differs among plant components (Tyree et al. 1991, Cochard et al. 1992, Tyree et al. 1993*a*, Sperry and Saliendra 1994). In *Betula occidentalis* Hook., distal portions were less vulnerable to cavitation, i.e., petioles were less vulnerable than stems and

stems less vulnerable than roots (Sperry and Saliendra 1994). In contrast, in *Juglans regia* L., petioles were more vulnerable to cavitation than stems (Tyree et al. 1993*a*). Similarly, in *Acer saccharum* Marsh., minor twigs were more vulnerable to cavitation than larger stems (Tyree et al. 1991). However, no difference in vulnerability was detected in three *Quercus* species (Cochard et al. 1992). These variations might reflect different adaptive mechanisms, which would be better understood with additional knowledge of R_{plant} and its components.

In this study, we report (1) a comparison between the HPFM and EF methods for measuring hydraulic resistances of plants, and (2) within plant variations in xylem vulnerability to cavitation in *Acer saccharinum* L.

Materials and methods

Acer saccharinum grows to between 18 and 24 m high and 0.6 to 0.9 m in diameter and usually has a short bole that divides near the ground into several upright branches. The crown is wide-spreading, and the root system is shallow. It is a characteristic bottomland species of the eastern United States, where it is not found on dry soils; however, planted trees seem to do well even on dry clay soils.

At various times during 1994 and 1995, *Acer saccharinum* seeds were germinated on wet filter paper in a greenhouse at the USDA Forest Service, Northeastern Forest Experiment Station, Burlington, Vermont. After radicals emerged, seeds were planted in 0.2 dm^3 pots. The seedlings were transplanted to 2.7 and 5.8 dm^3 pots as they grew larger. Soil medium consisted of a 50/50 (v/v) mix of vermiculite and sifted peat moss. Experiments were done on four sets of seedlings designated as the May, September, November and December plants according to the month in 1995 when measurements were conducted. The plants of the first three sets were 0.6 to 1.2 m high and 7 to 14 mm in basal diameter (including bark) and in 2.7 and 5.8 dm^3 pots. The December plants were 0.2 to 0.4 m high and 2.0 to 4.8 mm in basal diameter and in 0.2 dm^3 pots. The plants were six to twelve months old and usually had no branches, i.e., all leaves were on the main stem. The vulnerability of xylem to cavitation was assessed in May and September plants, whereas plant hydraulic resistance was measured in September, November and December plants. In June and July 1995, vulnerability was also measured in native plants growing on the shore of Lake Champlain, near Oakridge Park, South Burlington, Vermont. They were about 5 m high and 0.2 m in basal diameter.

Percent loss of hydraulic conductivity

Percent loss of hydraulic conductivity, PLC, was measured on petiole, stem and roots segments as described by Sperry et al. (1988). Briefly, segments were excised under water and connected to a conductivity apparatus. Initial conductivity, K_i (kg m s^{-1} MPa^{-1}) was measured with a pressure difference, P, of 0.006 MPa, using 10 mM oxalic acid, degassed and filtered through a 0.1 µm filter. The value of K_i was calculated from wL/P, where L is the length of the segment (m) and w is the solution flow rate (kg s^{-1}). The segments were then flushed

with solution at a pressure of 0.17 MPa for 60 min to dissolve air bubbles, and hydraulic conductivity was determined again. From preliminary experiments, one flush was sufficient to obtain maximum conductivity, K_m (kg m s^{-1} MPa^{-1}), therefore, the value of the second measurement was treated as K_m. Percent loss of hydraulic conductivity was calculated from $100(1 - K_i/K_m)$.

Vulnerability curves

A vulnerability curve, VC, is the relation between minimum xylem water potential reached during dehydration and the corresponding PLC. Vulnerability curves of stems and petioles were constructed by dehydrating shoots. For native trees, shoots 1.5 to 2 m long were excised in the morning and then recut under water. The shoots, immersed under water at the base and covered with black plastic bags, were brought to the laboratory. Greenhouse-grown plants were also brought to the laboratory from the Forest Service greenhouse. The shoots of the greenhouse-grown plants were excised in the laboratory. Deionized water at a pressure of 0.6 MPa, filtered through a 0.1 µm filter, was directed to the base of the shoots of both native and greenhouse-grown plants for 4 h to eliminate the embolisms in shoots of plants in the native state. Before perfusion, the native embolism of petioles was up to 75% of PLC and was reduced to 20 to 30% during perfusion, while stem PLC was reduced from about 20% to less than 10%. After the perfusion, the shoot was enclosed in a pressure chamber with the base protruding to the outside through a rubber seal. Different shoots were pressurized for 14 h at different gas pressures. At the end of the pressurization period, the shoot was removed from the pressure chamber, placed under water, and stem and petiole segments 20 mm long were excised. Stem segments were excised from a current-year stem where the bark was still green. All bark was removed and PLC was then measured as described above.

Root VC was constructed only for greenhouse-grown plants. We used two procedures to pressurize the roots. Some plants were transplanted to small cylindrical pots, 6.5 cm in outside diameter and 32 cm high, that fitted inside a pressure chamber. Two to 4 weeks after transplanting, the shoot was excised and the pot with root and soil was placed in the chamber with the 0.2-m-long stem base protruding to the outside through a rubber seal. The time of pressurization was 17 to 24 h. For the other plants, the roots were separated from the soil hydraulically and pressurized at selected pressures for 14 h by the same procedure described for shoots. The roots pressurized with and without soil were referred to as potted and bare, respectively. After pressurization, the roots were removed from the pressure chamber and PLC was measured on root segments (1.1 to 2.7 mm diameter and 20 mm long) as described above. The VC of bare roots was constructed from May and September plants and that of potted roots of September plants.

Evaporative flux densities

Evaporative flux density, E, was measured gravimetrically. Differences in evaporative flux densities were induced by changing the electric current to the lamp and the distance

between the lamp and plants. Air temperature was about 23 °C. Pots were watered and enclosed in plastic bags to prevent evaporation from soils, and placed on a digital balance. A computer recorded the rate of water use by reading the balance weight over time. Values of E were calculated from $\Delta W/(A\Delta t)$ where ΔW = the weight change (kg) in Δt (s), and A = leaf area (m^2), which was determined at the end of the experiments.

Leaf and stem water potentials

Leaf and stem water potentials (Ψ_{leaf} and Ψ_{stem}) were measured with a pressure chamber (PMS Instrument Co., Corvallis, OR). Stem water potential was equated to the water potential measured in the middle third of the canopy on a leaf covered with aluminum foil to prevent transpiration (Begg and Turner 1970). Two hours was sufficient to obtain steady-state water potentials after exposure to light.

Evaporative flux (EF) values of root and shoot resistance

At the steady state, the resistance from root to leaf, R_{plant} or $R_{root + shoot}$, and from root to stem, $R_{root + stem}$, were calculated from:

$$R_{plant} = -(\Psi_{leaf} - \Psi_{soil})/E$$

$$R_{root + stem} = -(\Psi_{stem} - \Psi_{soil})/E,$$

where Ψ_{soil} was the water potential at the soil–root interface and was taken as Ψ_{stem} and Ψ_{leaf} measured on bagged, or nontranspiring plants. For determination of Ψ_{soil}, two to five plants per set were sealed in a black plastic bag for 12 to 14 h and water potentials measured with a pressure chamber.

High-pressure flowmeter (HPFM) values of root and shoot resistance

Shoot resistance, its components and R_{root} were measured by the HPFM method (Yang and Tyree 1994, Tyree et al. 1994*c*, 1995). Wounds caused by the EF method during water potential measurements were sealed by epoxy, then shoots were excised from roots under water. The HPFM was connected first to the root and resistance was measured by three transients as described in Tyree et al. (1995). Briefly, in the transient measurement, pressure applied to the root was increased at 5 kPa s^{-1} and the pressure and flow rate were recorded every 4 s. Hydraulic conductance was calculated from the slope of the plot of flow versus applied pressure. Hydraulic resistance was the reciprocal of conductance. Tyree et al. (1994*c*, 1995) have published a detailed discussion of the theory of dynamic measurements of hydraulic resistance and quantitative verification that such measurements are free of errors from hysteresis effects, tissue capacitance, tissue elasticity, and air-bubble compression.

Next, the HPFM was connected to the base of the shoot. Shoots were perfused for 20 to 40 min at a pressure of 0.5 MPa with deionized water that had been degassed and filtered through a 0.1 μm filter. Shoots were then recut by 3 to 7 cm from the base to remove the plugged section caused by the first perfusion, and perfused again for 10 to 15 min. Preliminary measurements revealed that the recutting removed the plugged section caused by the first perfusion and that plugging during the second perfusion was slight (typically < 5%). We also determined the conductivity of 15-cm-long stem segments from different plants, which served as controls, using the conductivity apparatus described previously. The comparison revealed that stem resistance in unrecut material was more than twice that in the control stem segments and the difference was statistically significant ($P = 0.0076$). When the stem base was recut, the average value of resistance determined by the HPFM was 20% larger than that of the control, but the difference was not statistically significant ($P = 0.31$).

Shoot resistance was measured by one transient. Transients were performed twice more, once after removal of leaf blades and once after removal of petioles. At the end of the measurements, the leaf areas of the shoots were measured with an LI-3100 leaf area meter (Li-Cor, Inc., Lincoln, NE). All values were normalized by multiplying resistance by leaf area (Yang and Tyree 1993). Resistances of the shoot components were calculated from the difference between resistances before and after removal of each component.

Statistical analysis was made with the SigmaPlot 2.0 and SigmaStat ver. 1.0 for windows software packages (Jandel Scientific Software, San Rafael, CA). Resistance values were compared by the Student's *t*-test and differences were considered statistically significant at $P = 0.05$. Vulnerability curves were fit by the least squares methods based on an empirical function $y = a/(1 + \exp(b(x - c)))$, where y = PLC and x = water potential. The coefficients are a = maximum PLC, b = coefficient determining slope of sigmoid curve, and c = water potential at PLC = 50%. Otherwise, linear regression analysis was used.

Results

There was no correlation between basal diameter (3.3−11.3 mm) of the plants and R_{plant} (data not shown), which justified pooling data from plants over the range of basal diameters used in this study.

Leaf water potential of non-transpiring plants averaged −0.04 MPa and was considered to be equivalent to Ψ_{soil}. Water potential changes, $\Delta\Psi$, across plant organs were measured directly with a pressure chamber (EF method) or computed from the product of evaporative flux density, E, and resistance of the organ (measured with the HPFM). The relationships between E and $\Delta\Psi$ are plotted in Figure 1. The water potential drop from root to leaf, $\Delta\Psi_{root + shoot}$, increased linearly with increasing E (Figure 1a). The resistances calculated from the regression were 2.2×10^4 and 2.6×10^4 MPa m^2 s kg^{-1} for the HPFM and the EF methods, respectively. The water potential drop across root and stem, $\Delta\Psi_{root + stem}$, also increased linearly with increasing E (Figure 1b). The calculated resistances were similar between the two methods and averaged 1.9×10^4 MPa m^2 s kg^{-1}. On the other hand, values of $R_{petiole + leaf}$ were larger when determined by the EF method than by the HPFM method; furthermore, the data determined by the EF method were rather variable (Figure 1c). The $R_{petiole + leaf}$ was 6.8×10^3
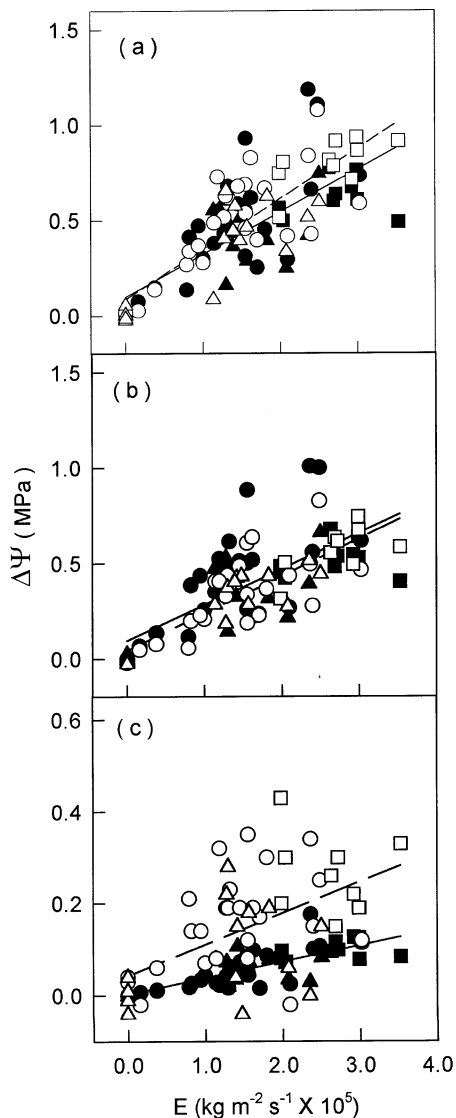
Figure 1. Water potential drop ($\Delta\Psi$) versus evaporative flux density (E) across whole plant (a), across root and stem (b) and across petioles and leaves (c) of *Acer saccharinum*, determined by the high-pressure flowmeter, HPFM, (closed symbols) and evaporative flux, EF, (open symbols) methods. Circles, squares and triangles indicate September, November and December plants, respectively. Regression lines are: (a) HPFM: $\Delta\Psi = 0.100 + 22296E$, $r^2 = 0.55$; EF: $\Delta\Psi = 0.087 + 26361E$, $r^2 = 0.71$; (b) HPFM: $\Delta\Psi = 0.097 + 18740E$, $r^2 = 0.50$; EF: $\Delta\Psi = 0.044 + 19566E$, $r^2 = 0.71$; (c) HPFM: $\Delta\Psi = 0.002 + 3557E$, $r^2 = 0.62$; EF: $\Delta\Psi = 0.042 + 6795E$, $r^2 = 0.26$.

versus 3.6×10^3 MPa m^2 s kg^{-1} for the EF and HPFM methods, respectively. Therefore, the relationship between E and $\Delta\Psi$ was similar between the two methods, except for E and $\Delta\Psi_{\text{petiole + leaf}}$.

The resistances were calculated individually and analyzed by the paired t-test to determine significant differences between the methods (Table 1). The comparison was limited to plants with $E > 0.8 \times 10^{-5}$ kg m^{-2} s^{-1}. There was no significant difference in $R_{\text{root + shoot}}$ or $R_{\text{root + stem}}$ between the two methods. There was a significant difference in $R_{\text{petiole + leaf}}$ between the

Table 1. Whole-plant hydraulic resistance (R_{plant}), resistance across both root and stem ($R_{\text{root + stem}}$) and both across petioles and leaves ($R_{\text{petiole + leaf}}$) of *Acer saccharinum*, determined by the high-pressure flowmeter (HPFM) and evaporative flux (EF) methods. Values are means $\pm$ SE ($n = 41$).

Plant component	Resistance		P^1
	HPFM ((MPa m^2 s kg^{-1}) $\times 10^{-3}$)	EF	
R_{plant}	30.9 ± 1.9	33.5 ± 1.7	NS
$R_{\text{root + stem}}$	27.1 ± 1.8	23.6 ± 1.1	NS
$R_{\text{petiole + leaf}}$	3.75 ± 0.25	9.9 ± 1.2	< 0.0001

[1] P = Probability value; NS indicates means not significantly different at 0.05 level of probability in paired t-test.

EF and HPFM methods; values obtained by the EF method were 2.6 times higher: 9.9×10^3 versus 3.8×10^3 MPa m^2 s kg^{-1}. Because R_{plant} is the sum of $R_{\text{root + stem}}$ and $R_{\text{petiole + leaf}}$, the higher values of $R_{\text{petiole + leaf}}$ resulted in higher values of R_{plant} by the EF method even though the EF values yielded lower values of $R_{\text{root + stem}}$.

Table 2 shows the component resistances of plants measured by the HPFM. Root resistance accounted for 66% of R_{plant}. Stem resistance was larger than R_{leaf} and R_{petiole}. Leaf resistance averaged 2.3×10^3 MPa m^2 s kg^{-1} or about $0.1 \times R_{\text{root}}$.

Several trends were observed in the vulnerability curves (Figure 2). (1) There were distinct differences in VC among plant structures. The petioles were most vulnerable and lost 50% of their hydraulic conductivity at -0.5 MPa. The roots were least vulnerable with a 50% loss of hydraulic conductivity at -2.2 MPa (based on a regression including all data). Vulnerability of stems was intermediate between the vulnerabilities of petioles and roots. Distal stem segments were more vulnerable than basal segments. (2) Stem segments were more vulnerable in May plants than in September plants. A similar but less distinct trend was observed in roots. There was no seasonal dependence in the vulnerability of petioles. (3) Vulnerability of stems and petioles from the native trees was variable. The range of variation in vulnerability of stem segments of native trees covered the seasonal range of variation of the greenhouse-grown plants. Vulnerability of native petioles tended to be less than that of petioles of greenhouse-grown

Table 2. Resistances of plant components and their contributions to whole-plant resistance in *Acer saccharinum*, measured by the high pressure flowmeter (HPFM) method. Values are means $\pm$ SE ($n = 41$).

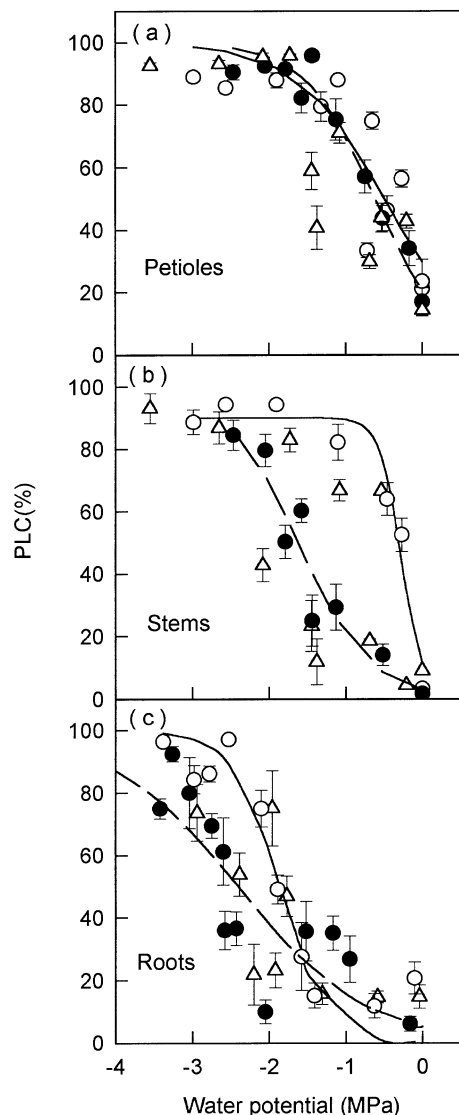| Plant component	Resistance ((MPa m^2 s kg^{-1}) $\times 10^{-3}$)	Contribution (%)
R_{shoot}	10.2 ± 0.8	34.0 ± 1.45
R_{leaf}	2.27 ± 0.20	7.7 ± 0.56
R_{petiole}	1.51 ± 0.12	5.4 ± 0.43
R_{stem}	6.44 ± 0.66	20.8 ± 1.41
R_{root}	20.6 ± 1.5	66.0 ± 1.45

Figure 2. Vulnerability curves, VC, for petioles (a), stems (b) and roots (c) of *Acer saccharinum*. Values are means of seven to ten segments and vertical bars are standard errors of the mean. Open and closed circles indicate values from May and September plants, respectively. Open triangles indicate values from native plants in (a) and (b), and from potted roots in (c). The regression lines apply to open (solid line) and closed circles (dashed line) only.

plants. (4) No difference in vulnerability was found between pressurized bare roots and pressurized potted roots.

Discussion

The HPFM and the EF methods yielded consistent values of plant hydraulic resistances except for $R_{\text{petiole + leaf}}$ (Figure 1 and Table 1). Leaf + petiole resistance values may differ because of differences in liquid-flow pathways or the condition of the pathways imposed by the two methods, or both. Yang and Tyree (1994) suggested that the HPFM underestimates resistances in plants with a high native state embolism. Petioles had

a native state embolism that was high enough to cause up to 75% loss of hydraulic conductivity. Because air bubbles dissolve during perfusion and are compressed during the transient measurement, the HPFM method might underestimate R_{petiole} by up to a factor of four. Underestimation of R_{petiole} could account for about half of the difference in resistance between the EF and HPFM estimates of $R_{\text{petiole + leaf}}$, which differed by 6×10^3 MPa m^2 s kg^{-1}. Because petioles were embolized in the native state, it is reasonable to assume that vessels in leaf blades were also embolized. Such embolism might account for the rest of the discrepancy between the methods. We do not know how much the $R_{\text{petiole + leaf}}$ values were affected by a difference in the hydraulic pathway of leaf blades induced by positive pressures during HPFM perfusion, and by negative pressures during normal transpiration (Yang and Tyree 1994).

Root resistance accounted for 66% of R_{plant} in *Acer saccharinum* and was within the range (20 to 90%) reported in other papers. The absolute value of R_{root} (= 2×10^4) of *Acer saccharinum* was at the lower end of the range of other species. For example, values of 2 to 4×10^4 MPa m^2 s kg^{-1} have been reported for other *Acer* species (Yang and Tyree 1994), 2.5 to 7.5×10^4 MPa m^2 s kg^{-1} for *Quercus* species (calculated from Èermak et al. 1980, Breda et al. 1993, Tyree et al. 1993*b*), and 5.7×10^4 for *Pinus contorta* Dougl. ex Loud. (Running 1980). However, it was seven times higher than the value of about 0.3 $\times 10^4$ MPa m^2 s kg^{-1} reported for *Betula occidentalis* (Sperry et al 1993). Because root and shoot resistances were comparable in these species, we conclude that R_{plant} of *Acer saccharinum* was relatively low compared with reported values.

The value of R_{leaf} (Table 2) was 10% of that of other *Acer* (Yang and Tyree 1994) and *Quercus* species (Tyree et al. 1993*b*), but it was only 50% less than that of *Juglans regia* (Tyree et al. 1993*a*). In contrast, R_{petiole} of *Acer saccharinum* was highest among these species except for *Betula occidentalis*. Thus, *Acer saccharinum* appeared to have a low R_{plant} and a low R_{leaf} compared with most other species.

Tyree et al. (1994*a*) compared the vulnerability to cavitation of 60 species and concluded that *Acer saccharinum* was one of the most vulnerable species (Figure 2), and was similar to *Populus deltoides* Bartr. ex Marsh. in terms of vulnerability differences among samples. Tyree et al. (1994*b*) proposed that genetic diversity might explain the variation in xylem vulnerability of *Populus deltoides*. However, genetic diversity may not play a role in the plants in this study because they all originated from the same halfsib seed lot. Although plant age was similar (10 to 12 months grown under greenhouse conditions), there were differences in growth conditions between the May and September plants. September plants were grown at higher temperature and solar irradiance than May plants, but environmental conditions in the greenhouse were not recorded. It is possible that xylem is less vulnerable to cavitation when differentiated under conditions of high temperature and irradiance. Such change can be caused by a decrease in the diameter of pores in inter-vessel pit membranes (Sperry et al. 1991).

Zimmermann (1983) proposed the plant segmentation hypothesis to explain adaptive features of plants to various environments. According to the hypothesis, small expendable

organs are sacrificed under unfavorable conditions. Tyree et al. (1993*a*) has elaborated the plant segmentation hypothesis to recognize two kinds of segmentation: hydraulic segmentation and vulnerability segmentation. Hydraulic segmentation occurs when hydraulic constrictions occur, i.e., when conductances of stem and leaf junctions are low or when leaf specific conductivity, K_L, declines toward the apex of plants. Hydraulic constrictions make xylem pressure potentials decline more rapidly toward the apex when water is flowing in the stems. However, hydraulic segmentation is effective only at high E because the water potential gradient along the plant axis is negligible at low E (Tyree et al. 1993*a*).

Tyree et al. (1991, 1993*a*) found that distal portions of some plants were more vulnerable to cavitation than basal portions and named this spatial pattern "vulnerability segmentation." Plants with vulnerability segmentation may sacrifice small expendable distal parts at zero E (i.e., when soil is dry and stomata are closed), because cavitation occurs more readily in the distal portion than in the basal areas even though the xylem tension is nearly the same throughout a plant when $E = 0$.

Although there have been few studies of plant hydraulic resistance combined with vulnerability curves, some patterns have emerged. Compared with plants with high R_{plant}, plants with low R_{plant} tend to be more vulnerable to cavitation and exhibit vulnerability segmentation. For example, *Quercus* species have no vulnerability segmentation (Cochard et al. 1992) and high R_{plant} (Tyree et al. 1993*a*), whereas *Juglans regia* (Tyree et al. 1993*a*) and *Acer saccharinum* (this study) have vulnerability segmentation and low R_{plant}. Also, *Acer saccharinum* is more vulnerable to cavitation than *Quercus* species. *Pinus contorta* has a high R_{plant} (Running 1980) and conifers tend to be less vulnerable than hardwoods (Tyree et al. 1994*a*). Among the species studied, *Betula occidentalis* is an exception. It had a low R_{plant} and was highly vulnerable to cavitation, with the basal portions of the plant more vulnerable than the apex.

These trends seem to show a tradeoff between vulnerability patterns and R_{plant}. Let us assume that plants have to sacrifice distal and expendable portions to survive under dry environments. If R_{plant} is low, a steep pressure gradient across the whole plant may not develop and so vulnerability segmentation will confine cavitation to the distal region. In plants with high R_{plant}, high E may induce a greater pressure drop, thus cavitation might develop at the distal portion without vulnerability segmentation. On the other hand, at the same E, Ψ_{leaf} is lower in plants with high R_{plant} than in plants with low R_{plant}. Less vulnerability in plants with high R_{plant} might be favored to prevent cavitation over normal ranges of E.

There is another pattern of vulnerability segmentation where the roots are more vulnerable than the petioles, e.g., in *Betula occidentalis* (Sperry and Saliendra 1994). High vulnerability in *B. occidentalis* was related to the large diameter of xylem conduits and thus low root resistance. The large diameter also permits low investment in xylem structure to obtain low resistance (Tyree et al. 1994*a*). Because water potential is higher in roots than in shoots during steady-state E, this pattern of hydraulic resistances and vulnerability segmentation guaran-

tees large water flow or water use when water is available. However, it does not provide an adaptive advantage in dry environments because the roots may die as a result of cavitation before the death of the leaves. This may explain why *Betula occidentalis* is strictly riparian.

In conclusion, the hydraulic properties of *Acer saccharinum* seem consistent with its adaptive behavior. Low R_{plant} assures high transpiration rates in the presence of sufficient water, even though the xylem is extremely vulnerable to cavitation. The pattern of vulnerability segmentation, where the distal portion is more vulnerable than the basal portion, provides the ability to conserve soil water by shedding leaves and allows the roots to survive on a dry soil. More information is needed to clarify the tradeoff between R_{plant} and xylem vulnerability to cavitation. In this context, the high-pressure flowmeter method is a powerful tool that can measure hydraulic resistances of a plant more quickly than the evaporative flux method.

References

Begg, J.E. and N.C. Turner. 1970. Water potential gradients in field tobacco. Plant Physiol. 46:343–345.

Boyer, J.S. 1985. Water transport. Annu. Rev. Plant Physiol. 36:473–516.

Breda, H., H. Cochard, E. Dreyer and A. Granier. 1993. Water transfer in a mature oak stand (*Quercus petraea*): seasonal evolution and effects of a severe drought. Can. J. For. Res. 23:1136–1143.

Èermak, J., H. Huzulak and M. Penka. 1980. Water potential and sap flow rate in adult trees with moist and dry soil as used for assessment of root system depth. Biol. Plant. 22:24–41.

Cochard, H., N. Breda, A. Granier and G. Aussenac. 1992. Vulnerability to air embolism of three European oak species (*Quercus petraea* (Matt) Liebl., *Q. pubescens* Willd., *Q. robur* L.). Ann. Sci. For. 49:225–233.

Edwards, W.R., P.G. Jarvis, J.J. Landsberg and H. Talbot. 1986. A dynamic model for studying flow of water in single trees. Tree Physiol. 1:309–324.

Hellkvist, J., G.P. Richards and P.G. Jarvis. 1974. Vertical gradients of water potential and tissue water relations in sitka spruce trees measured with the pressure chamber. J. Appl. Ecol. 11:637–667.

Kramer, P.J. 1983. Water relations of plants. Academic Press, New York, 489 p.

Rieger, M. 1989. Pressure- and transpiration-induced flow methods for estimating hydraulic resistance in peach. HortScience 24:648–650.

Roberts, J. 1977. The use of tree-cutting techniques in the study of the water relations of mature *Pinus sylvestris* L. J. Exp. Bot. 28:751–767.

Running, S.W. 1980. Field estimates of root and xylem resistances in *Pinus contorta* using root excision. J. Exp. Bot. 31:555–569.

Sperry, J.S. and W.T. Pockman. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. Plant Cell Environ. 16:279–287.

Sperry, J.S. and N.Z. Saliendra. 1994. Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. Plant Cell Environ. 17:1233–1241.

Sperry, J.S., J.R. Donnelly and M.T. Tyree. 1988. A method for measuring hydraulic conductivity and embolism in xylem. Plant Cell Environ. 11:35–40.

Sperry, J.S., A.H. Perry and J.E.M. Sullivan. 1991. Pit membrane degradation and air-embolism formation in aging xylem vessels of *Populus tremuloides* Michx. J. Exp. Bot. 42:1399–1406.

Sperry, J.S., N.N. Alder and S.E. Eastlack. 1993. The effect of reduced hydraulic conductance on stomatal conductance and xylem cavitation. J. Exp. Bot. 44:1075–1082.

Tyree, M.T. 1988. A dynamic model for water flow in a single tree: evidence that models must account for hydraulic architecture. Tree Physiol. 4:195–217.

Tyree, M.T. and J.S. Sperry. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Plant Physiol. 88:574–580.

Tyree, M.T. and J.S. Sperry. 1989. Vulnerability of xylem to cavitation and embolism. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40:19–38.

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., D.A. Snyderman, T.R. Wilmot and J.-L. Machado. 1991. Water relations and hydraulic architecture of a tropical tree (*Schefflera morototoni*): data, models, and a comparison with two temperate species (*Acer saccharum* and *Thuja occidentalis*). Plant Physiol. 96:1105–1113.

Tyree, M.T., H. Cochard, P. Cruiziat, B. Sinclair and T. Ameglio. 1993*a*. Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. Plant Cell Environ. 16:879–882.

Tyree, M.T., B. Sinclair, P. Lu and A. Granier. 1993*b*. Whole shoot hydraulic resistance in *Quercus* species measured with a new high-pressure flowmeter. Ann. Sci. For. 50:417–423.

Tyree, M.T., S.D. Davis and H. Cochard. 1994*a*. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? IAWA J. 15:335–360.

Tyree, M.T., K.J. Kolb, S.B. Rood and S. Patiño. 1994*b*. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem? Tree Physiol. 14:455–466.

Tyree, M.T., S. Yang, P. Cruiziat and B. Sinclair. 1994*c*. Novel methods of measuring hydraulic conductivity of tree root systems and interpretation using AMAIZED: a maize-root dynamic model for water and solute transport. Plant Physiol. 104:189–199.

Tyree, M.T., S. Patiño, J. Bennink and J. Alexander. 1995. Dynamic measurements of root hydraulic conductance using a high-pressure flowmeter in the laboratory and field. J. Exp. Bot. 46:83–94.

Yang, S. and M.T. Tyree. 1993. Hydraulic resistance in *Acer saccharum* shoot and its influence on leaf water potential and transpiration. Tree Physiol. 12:231–242.

Yang, S. and M.T. Tyree. 1994. Hydraulic architecture of *Acer saccharum* and *A. rubrum*: comparison of branches to whole trees and the contribution of leaves to hydraulic resistance. J. Exp. Bot. 45:179–186.

Zimmermann, H.M. 1978. Hydraulic architecture of some diffuse-porous trees. Can. J. Bot. 56:2286–2295.

Zimmermann, H.M. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo, 143 p.