

Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem?

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Received February 22, 1993

Summary

Vulnerability of xylem to loss of hydraulic conductivity caused by drought-induced cavitation was determined for three riparian cottonwood species in Lethbridge, Alberta: *Populus deltoides* Bartr., *P. balsamifera* L., and *P. angustifolia* James. These species suffered 50% loss of hydraulic conductivity in one-year-old stem segments when xylem pressure potential fell to -0.7 MPa for *P. deltoides* and -1.7 MPa for *P. balsamifera* and *P. angustifolia*, making them the three most vulnerable tree species reported so far in North America. The possible contribution of drought-induced xylem dysfunction to the decline of riparian ecosystems in dammed rivers is discussed.

Keywords: *Populus*, riparian ecosystems, water stress.

Introduction

The cottonwood (poplar) forests that line the river valleys of the western prairies and mountain foothills are aesthetically and recreationally valuable, and particularly rich wildlife habitats (USDA Forest Service 1977). However, although historically abundant, these forests have been declining rapidly. It is estimated that three-quarters of the cottonwood forests in the American southwest have already been lost (Johnson and Haight 1984). The decline of these woodlands has prompted the World Wildlife Fund, Canada to designate riparian cottonwood forests as one of North America's most threatened ecosystems (Canadian Parks and Wilderness Society 1990).

One negative impact on the cottonwoods that is already widespread and continually increasing is that due to damming and water diversion. Several recent studies have independently revealed the decline of riparian cottonwoods downstream from dams (reviewed in Rood and Mahoney 1990). In extreme cases, forest decline can be abrupt and almost complete (Stine et al. 1984, Rood and Heinze-Milne 1989, Snyder and Miller 1991).

Cottonwoods grow in sand-gravel soils no more than 4 m above the water level in river valleys 20 to 50 m deep and 0.3 to 3 km wide. The soil water table closely tracks the river level (Mahoney and Rood 1991b), and it has been argued that forest decline downstream from some dams is a consequence of insufficient flows during the

summer months when water is diverted off-stream for irrigation or other uses (Rood and Mahoney 1990). Mortality may follow particularly abrupt reductions in river flows because the adjacent riparian water table would probably also drop quickly, creating acute drought stress.

Additional studies of the water relations, vulnerability to cavitation, and hydraulic architecture of riparian cottonwoods may provide new insights about the way drought contributes to the decline of ecosystems downstream from dams. A better understanding of the drought responses of cottonwoods could guide development of in-stream flow regimes compatible with the survival of riparian forests (Mahoney and Rood 1991a, Stromberg and Patten 1991).

Recently it has been shown that eastern provenances of *Populus deltoides* are more vulnerable to xylem cavitation events than other North American tree species (Tyree and Ewers 1991, Tyree et al. 1992). Cavitation events are induced when xylem pressure potential, Ψ_{xp} , becomes negative enough during drought stress to suck air bubbles into previously water-filled xylem vessels (Cochard et al. 1992). The xylem dysfunction resulting from the presence of air bubbles causes a reduction in stem hydraulic conductivity. Reduced conductivity can persist for the rest of the growing season, because embolism collapse requires periods of positive Ψ_{xp} (Tyree and Yang 1992), and this rarely occurs during the growing season. If the loss of hydraulic conductivity is too great, leaf water potential, Ψ_{leaf} , and turgor can fall sufficiently to reduce growth rate and cause partial stomatal closure during midday and reduced net assimilation. In extreme cases, xylem cavitation can cause death of shoots. Thus, when the water table is too low as a consequence of damming, or when it declines too rapidly, the resulting water stress may promote the decline of the riparian cottonwoods.

The objectives of this preliminary study of riparian cottonwoods in Alberta were: (1) to measure cottonwood vulnerability to drought-induced xylem dysfunction, (2) to determine the amount of xylem dysfunction in the native state, and (3) to determine whether midday Ψ_{xp} is sufficiently negative to cause xylem dysfunction in the native state.

Materials and methods

Plant material

Experiments were conducted on trees of *Populus angustifolia* James, *P. balsamifera* L., and *P. deltoides* Bartr. growing in the Oldman River valley adjacent to the University of Lethbridge, Lethbridge, Alberta. The site was mainly occupied by stands of a single species or natural hybrid. The site can be classified as a riparian ecosystem in the early stages of decline.

Percent loss of hydraulic conductivity (native state)

Percent loss of hydraulic conductivity, PLC, was measured on one-year-old stem segments 18 to 22 mm long and 2 to 4 mm in wood diameter. Shoots 1 to 1.5 m long

and 10 to 20 mm in basal diameter were excised from trees, immediately taken to the laboratory and recut under water. Stem segments just below the current-year leaf-bearing stems were excised under water and mounted in a conductivity apparatus described elsewhere (Sperry et al. 1987). Initial hydraulic conductivity, K_i , was determined by measuring the solution flow rate (kg s^{-1}) perfused through the segment at a pressure drop of about 5 kPa. The solution consisted of 100 mM KCl, degassed and filtered through a $0.1 \mu\text{m}$ filter. Subsequently, the segments were 'flushed' with the same solution at a pressure of 150 kPa for 10 to 20 min. The flush dissolved air bubbles in the vessels causing an increase in hydraulic conductivity. The hydraulic conductivity was remeasured at a pressure drop of 5 kPa. The process was repeated until a maximum hydraulic conductivity, K_{max} , was achieved, usually after one or two flushes. PLC was calculated from

$$\text{PLC} = 100(K_{\text{max}} - K_i)/K_{\text{max}}. \quad (1)$$

Vulnerability curves

A vulnerability curve is a plot of the PLC of stem segments versus the Ψ_{xp} inducing the observed PLC. Various methods of measuring vulnerability curves are described elsewhere (Sperry et al. 1987, Tyree et al. 1992, Cochard et al. 1992). Vulnerability curves were measured on excised branches 1 to 1.5 m long and 8 to 15 mm in basal diameter. Initial observations of high PLCs in branches brought in from the field indicated that the branches had already experienced considerable water stress or a carryover of embolisms from winter desiccation. The preexisting embolisms prevented determination of the vulnerability curve in the range of high Ψ_{xp} . Branches were first pressure infiltrated to remove native embolisms, on the assumption that refilled xylem vessels would recavitate at the same Ψ_{xp} values that caused cavitation in the native state. Tap water at a pressure of 200 to 300 kPa was directed through tygon tubing to a $0.1 \mu\text{m}$ filter then through another length of tygon tubing to the base of the excised shoot (1 to 2 m long). *Populus deltoides* and *P. angustifolia* shoots were perfused for 4 h and *P. balsamifera* for 18 h. During perfusion, leaf air spaces were infiltrated with water and water dripped from the stomata.

After the initial perfusion, the shoots were removed from the water source and slowly dehydrated on the bench top under laboratory lighting. Different periods of dehydration resulted in different values of Ψ_{xp} , as determined by measurements on four excised leaves made with a pressure chamber (PMS Instrument Co., Corvallis, Oregon). The shoots were placed in plastic bags with moist towels for 2 to 3 h after the determination of Ψ_{xp} to allow recently cavitated vessels to embolize fully without further dehydration. The shoots were then placed under water, stem segments were excised, and PLC measured as described above.

Field measurements of Ψ_{leaf} and transpiration

On a few sunny days in June and July 1992, field measurements of midday Ψ_{leaf} were made on excised leaves with a pressure chamber, after which evaporative flux density, E ($\text{kg s}^{-1} \text{m}^{-2}$) was measured with a model LI1600 porometer (Li-Cor Inc.,

Lincoln, Nebraska). These measurements were made to estimate Ψ_{xp} of one-year-old stems to see if native state PLCs could be accounted for by measured vulnerability curves. Under field conditions in trees with high E , Ψ_{leaf} ought to be more negative than Ψ_{xp} of stems supplying water to the leaves because of the effect of resistance to water flow in apical stems and leaves. To estimate the magnitude of this effect, the resistance to water flow offered by leaf blades, petioles and current-year stems, R^* , was estimated as described below. The Ψ_{xp} value could then be calculated from

$$\Psi_{xp} = \Psi_{leaf} + ER^*. \quad (2)$$

Leaf and shoot resistances to water flow

Leaf and shoot resistances were measured with a new high pressure flowmeter, shown diagrammatically in Figure 1. The flowmeter permitted the perfusion of solution into the base of a branched system while measuring the flow rate, F (kg s^{-1}). The main body of the system was constructed from glass tubing, tygon tubing, stopcocks, and plastic T-junctions. The perfusion solution was held in a flexible plastic bag inside a reservoir and was placed under pressure by compressed air controlled with a pressure regulator. The solution, which was 100 mM KCl filtered through a $0.1 \mu\text{m}$ filter, was directed through a capillary tube (0.7 mm in diameter and 0.12 m long) to the shoot. The rate of flow, F , across the capillary tube was proportional to the pressure drop across the tube. The pressure drop was recorded with a two-arm water manometer made from thick-walled glass capillary tubes of 1.5 mm internal diameter. The solution in the right arm of the manometer was always at the same level as the solution in the reservoir. Air spaces over the solution in the reservoir and in the two arms of the manometer were connected by tygon tubing to equalize the pressure. This prevented the solution in the right manometer from rising above the level of solution in the reservoir when the solution was under pressure. The level of solution in the left manometer depended on the rate and direction of flow

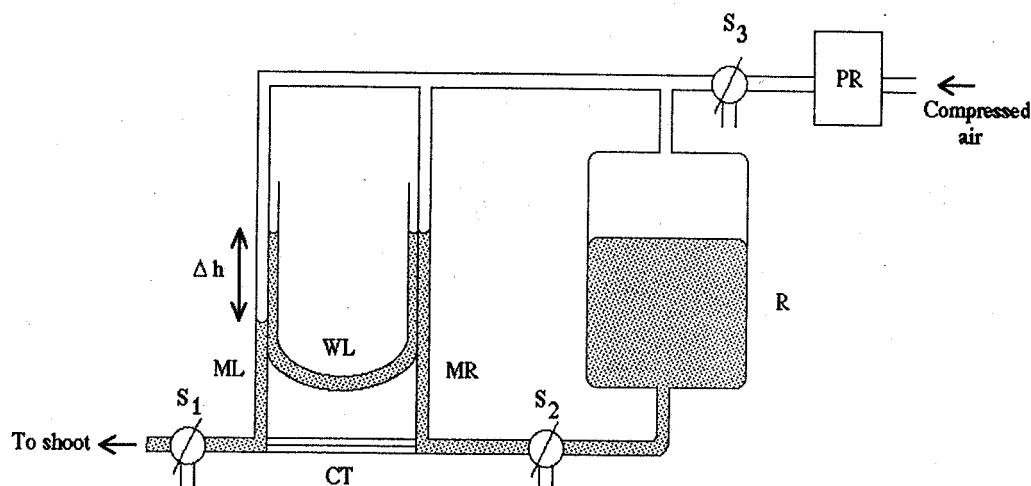


Figure 1. Diagrammatic representation of the high-pressure flowmeter used for measuring shoot resistance to water flow. See text for details.

across the capillary tube. Usually, the flow was from right to left (Figure 1), which made the level in the left arm of the manometer lower than that in the right arm. To facilitate more accurate measurement of the height difference, Δh , between the two arms, a water level was used to transfer the level of solution from the right arm of the manometer to the left arm. The water level consisted of a length of tygon tubing partly filled with solution. The position of the tubing was adjusted so that the level of solution in the water level was the same as that in the right arm of the manometer; then Δh could be measured at the place shown in Figure 1. Three-way stopcocks (S_1 and S_2) were used to fill the flowmeter and reservoir with solution, and S_3 was used to release air pressure from the system.

The flowmeter was calibrated by directing the flow of solution across a length of stem segment via solution-filled tubing to a container of solution on a balance. Flow rate, F , was adjusted to different values by changing the air pressure in the reservoir and measuring the rate of flow (kg s^{-1}) into the container of solution on the balance. A typical calibration curve is shown in Figure 2. The difference in solution levels, Δh , was rarely 0 at $F = 0$, because of differences in surface tension between the solution in the right arm and the left arm of the manometer. This happened because it was not possible to keep the capillary tubes perfectly clean. There was usually a height difference, Δh_0 , of a few mm at $F = 0$, but this difference rarely changed more than 1 or 2 mm from the beginning to the end of an experiment. All flow rates were calculated from the slope of the calibration curve (Figure 2) after correcting Δh for Δh_0 .

The problem of a nonzero Δh_0 could have been eliminated by replacing the manometer columns with a differential pressure gauge like that used in a low-pressure flowmeter described by Tyree (1983). That, however, would have eliminated the main advantages of the present high-pressure flowmeter, i.e., that it was inexpensive and could be used without a power source under field conditions. Using larger bore capillary tubes for the left and right arms of the manometer would have reduced the size of Δh_0 , but would also have increased the response time. The system used in this

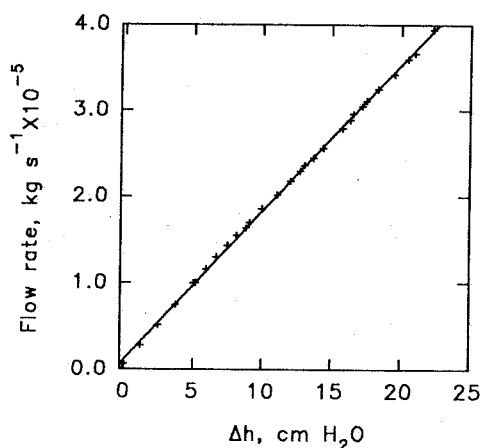


Figure 2. Typical calibration curve of the high-pressure flowmeter shown in Figure 1. The x-axis is the height difference between the right and left manometer columns shown in Figure 1.

study took about 30 s to adjust to a stable Δh in response to a rapid change in F during calibration.

Shoot resistances were measured by connecting the flowmeter to a shoot (1.5 to 2 m long and 12 to 16 mm in basal diameter) and perfusing the shoot with 100 mM KCl at 0.2 MPa pressure for 2 or 3 h. Initially, flow rate was high and then gradually declined. The high initial flow rate was attributed to negative leaf water potentials, Ψ_{leaf} . But after 2 or 3 h, the leaf air spaces became infiltrated with water, water dripped from the stomata of some leaves and F became stable. Shoot resistance (R_s) was computed from

$$R_s = PA/F, \quad (3)$$

where P was the applied water pressure and A was the total leaf area of the shoots measured at the end of the experiment with a model LI3000 leaf area meter (Li-Cor Inc., Lincoln, Nebraska). Normalization of R_s by multiplying P/F by A was justified because preliminary experiments revealed that large shoots (with large A) had smaller values of P/F than small shoots; see Yang and Tyree (1993) for a discussion of how P/F depends on branch size in *Acer saccharum*.

Resistances of the components of a shoot were measured by making resistance measurements after removal of each component. For example, the resistance of the whole shoot was measured before and after removal of leaves and current-year shoots. The resistance of the leaf blade plus the petiole plus the current-year shoot (R^*) was calculated from

$$R^* = R_s - R_f, \quad (4)$$

where R_f is the final resistance of the shoot after apical components were removed.

Results

The vulnerability curves of the three riparian cottonwoods are shown in Figure 3A. Vulnerability curves have been measured for more than 40 species of trees worldwide. Among the temperate-zone species tested, the cottonwoods investigated here have the highest vulnerability to drought-induced xylem dysfunction (see also Sperry and Tyree 1990, Tyree and Ewers 1991). Each point in Figure 3A is the mean PLC for an individual shoot from which 10 stem segments were collected for measurement of PLC. Vertical error bars are standard errors of the means and horizontal error bars are standard deviations of Ψ_{leaf} measured on four leaves collected from each shoot after dehydration on a bench top.

All vulnerability curves in Figure 3A were fitted with second order polynomial lines. The PLC at $\Psi = 0$ was the PLC observed after perfusing the entire shoots with tap water to remove native embolisms. This pretreatment was evidently not totally successful because mean PLCs of 8 to 15% were observed. The regression lines in Figure 3A do not include the suspect PLC points on the right side of the graph. The

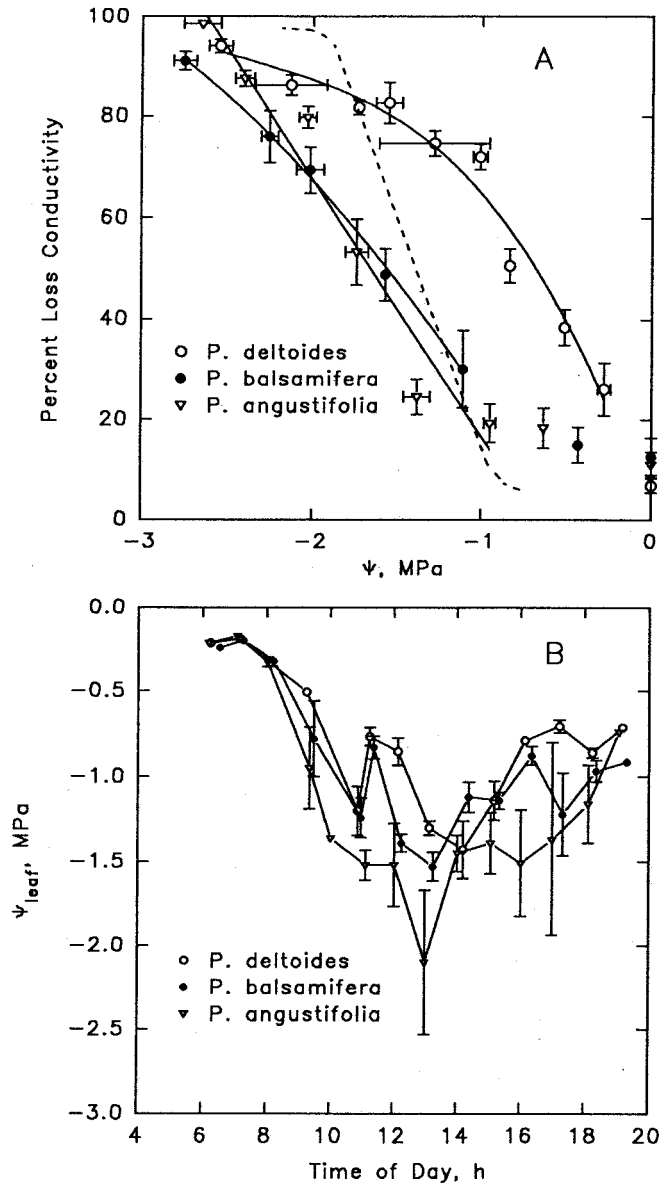


Figure 3. A: Vulnerability curves for three riparian cottonwoods. Each point is the mean \pm SEM percent loss hydraulic conductivity measured on 10 one-year-old stem segments excised from a branch dehydrated in the laboratory to the water potential shown on the x-axis. The horizontal error bars are the SD of four leaves measured in a pressure chamber. B: Diurnal time course of leaf water potential in three riparian cottonwoods measured under field conditions on a sunny day in July 1992.

vulnerability curves of *P. balsamifera* and *P. angustifolia* were quite similar. The vulnerability curve of *P. deltoides* from the Lethbridge provenance was shifted to the right, i.e., this species was more vulnerable compared with coppice material or rapidly growing cuttings from eastern provenances; see dashed line reproduced from Tyree et al. (1992). The vulnerability curves were remeasured in Vermont on *P. deltoides* samples collected from mature trees (Alexander and Tyree, unpublished data) and the vulnerability curve were found to be intermediate between those of *P. deltoides* and *P. balsamifera* in Figure 3A and somewhat more vulnerable than that determined on coppice material.

Diurnal time courses of Ψ_{leaf} of the three riparian cottonwoods on a sunny day in mid-July 1992 are shown in Figure 3B. Values plotted are means and standard deviations of Ψ_{leaf} measured on three leaves collected on the sunny side of the tree at each time shown on the x-axis. All species reached midday minimum values of about -1.5 MPa. Midday evaporative flux densities, E , ranged from 3.5×10^{-5} to $4.5 \times 10^{-5} \text{ kg s}^{-1} \text{ m}^{-2}$ from 1100 to 1400 h based on 10 to 15 measurements on individual leaves of each species. The Li-Cor LI1600 porometer alters the microenvironment of the leaves so the value of E might not reflect field values. Some people use the Li-Cor to measure leaf conductance, g_l , then estimate E from g_l , and independent estimates of leaf and air temperatures and air humidity. But this approach is also in error because the Li-Cor LI1600 incorrectly measures the leaf temperature used to calculate g_l (Tyree and Wilmot 1990). We tried measuring E with a whole-shoot potometer as described by Tyree et al. (1991), but the excised end of the shoots plugged up and stomata closed. In other species, we have generally found that the Li-Cor LI1600 overestimated E by up to 30% compared to values measured with a potometer on excised shoots in the field.

The resistance to water flow, R^* , in current-year shoots plus leaves and petioles was determined on two shoots collected from *P. angustifolia* and two shoots of a *P. deltoides* \times *balsamifera* hybrid. The R^* values were comparable and were pooled to yield a mean standard deviation of $4.6 \times 10^3 \pm 0.8 \times 10^3 \text{ MPa m}^2 \text{ s kg}^{-1}$. Five additional *P. deltoides* shoots, collected and measured in Vermont, had an R^* value of $3.3 \times 10^3 \pm 0.3 \times 10^3 \text{ MPa m}^2 \text{ s kg}^{-1}$. The product of $E \times R^*$ gave the likely drop in Ψ of ≤ 0.2 MPa, so midday values of Ψ_{xp} were probably -1.3 to -1.4 MPa in one-year-old stems.

Native state values of PLC on the three riparian cottonwoods are shown in Figure 4. The PLC values were plotted as means and standard deviations versus the date of collection; results from the 1992 and 1993 field seasons were pooled. There was no significant trend in PLC during the two field seasons which were wetter than average for Lethbridge, Alberta.

Discussion

Assuming that all one-year-old stem segments reached midday Ψ_{xp} of -1.3 MPa, we predicted likely native state values of PLC from the vulnerability curves in Figure 3A. The predicted values were approximately 35 and 41% for *P. angustifolia* and *P. balsamifera*, respectively. These predictions were within the range of values observed in Figure 4. A possible exception was *P. deltoides*; at -1.3 MPa, the predicted PLC was 76% based on the vulnerability curve in this study. Early season PLCs were in the range of 45 to 80%. Late season PLCs were more similar to the vulnerability curve of *P. deltoides* measured in Vermont (Tyree et al. 1992). There are two likely explanations for the differences in the vulnerability curves between Alberta and Vermont: (1) variability in vulnerability curves within a hybrid swarm may be genetically based or (2) vulnerabilities may change with the age of vessels. There are few studies of the genetic variability of vulnerability curves in hybrids, but

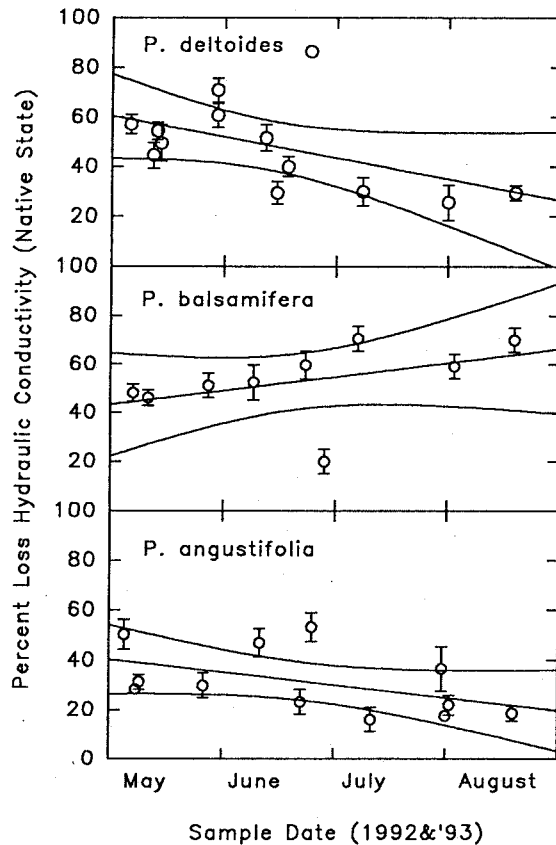


Figure 4. Native state values of percent loss of hydraulic conductivity (PLC) observed in one-year-old stem segments excised from three species of riparian cottonwoods on the dates indicated on the x-axis. The PLCs are given as means \pm SEM ($n = 10$ to 20).

varietal differences have been reported in vulnerability curves of sugarcane (Neufeld et al. 1992). All vulnerability curves in this study were measured on branches from a single individual, so the amount of genotypic variability is unknown. Pit membrane degradation in *P. tremuloides* causes old vessels to be more vulnerable to cavitation than recently formed vessels (Sperry et al. 1991). The vulnerability curves in this paper were all measured on 'one-year-old' stems, but the vulnerability curve for *P. deltoides* in this paper was measured early in the season when the majority of vessels were those formed in the previous growing season. The other vulnerability curves in Figure 3A were measured later in the season when most of the vessels present had been formed in the current growing season.

The exact value of PLC obtained in any given branch will depend on a complex of factors that include possible variation in the vulnerability curve from tree to tree, or even from branch to branch within a tree, and variation in the minimum Ψ_{xp} reached in any given branch. The minimum Ψ_{xp} reached will be determined by differences in microclimate within the crown of a tree (especially differences in irradiance caused by variation in the amount of mutual shading) and the branch to branch variation in hydraulic resistances to water flow. Some of the native value of the PLC may have been carried over from the previous growing season if embolisms were not fully dissolved in early spring before bud break.

There are several possible reasons for the absence of a strong seasonal trend in PLC. Both the 1992 and 1993 growing seasons were unusually wet so Ψ_{xp} may not have reached the extremes found in dry years. Cottonwoods are phreatophytes, i.e., some roots are always below the water table, so Ψ_{xp} could not be expected to track the progressive drop in Ψ in the upper soil layers. Finally, progressive loss of conductivity in older vessels may have been continuously compensated by the growth of new vessels as the season progressed.

The contribution of cavitation and consequent loss of hydraulic conductivity to the decline of riparian cottonwood ecosystems is unclear. Cottonwood species do not die in one growing season. The decline observed in Alberta is spread over 10 to 20 years and is characterized by a gradual dieback of the crown. If cavitation were the primary cause of crown dieback, then we would expect affected branches to die during the driest months of August and September. Surveys of riparian cottonwood decline have primarily involved air photo-surveys made on a single, relatively arbitrary date in the summer. The air photographs do not enable investigation of seasonal patterns of branch and crown dieback, but studies along the tributaries of the Oldman River Basin in southwestern Alberta did indicate premature leaf senescence along many cottonwood branches during July and, particularly, August in the very dry year of 1988. Unfortunately, specific branches were not tagged and the association of premature senescence, cavitation and subsequent branch mortality remains speculative. Even if branches do not die during periods of maximum water stress, cavitation could still play a secondary role in the mechanism of crown dieback as explained below.

Cavitation probably causes a permanent loss of hydraulic conductivity within any given growing season. Embolisms in vessels will disappear only when Ψ_{xp} returns to near zero or positive values (Tyree and Yang 1992, Yang and Tyree 1992). Root pressure developed overnight could raise Ψ_{xp} to positive values, but root pressure measured at the base of a cottonwood tree would have to rise to > 0.1 MPa to raise Ψ_{xp} to > 0 MPa at the top of a 10 m tree. We have drilled holes into the base of trees and have found no evidence of exudation or root pressure (except for exudation associated with wood decay; Abell and Hursh 1931, Zeikus and Ward 1974). Pickard (1989) has recently suggested a mechanism whereby diurnal changes in shoot temperature could release enough symplastic water in minor twigs to cause brief periods of positive Ψ_{xp} , but so far there is no evidence that this actually happened because predawn Ψ_{leaf} tended to be < -0.1 MPa (Figure 3B).

It is not clear how much Ψ_{xp} of cottonwoods is influenced by soil dehydration because some roots always penetrate into the water table. Because stomata close when Ψ_{leaf} becomes sufficiently negative, water flow through drought-stressed trees should fall to very low values and Ψ_{xp} of all branches in the crown should approach Ψ_{soil} (Tyree et al. 1993). If the vulnerability curves of all branches in a tree were the same, then the entire tree should die during a single episode of drought. There are exceptions, however, in which stomatal response may not be adequate to prevent uncontrolled cavitation in branches (see Sperry and Pockman 1993 and Sperry et al. 1993). Patchy dieback of the crown might be explained if particular branches are

supplied water by particular roots, i.e., if the hydraulic architecture of cottonwoods followed the unit-pipe model of a tree (Tyree and Ewers 1991). In that case, branches fed by shallow roots would be more water stressed than branches fed by deep roots as the upper soil layers progressively dried.

Another scenario for dieback is that loss of hydraulic conductance will cause reduced stomatal conductance for much of the day in affected branches and result in reduced net assimilation and reduced accumulation of carbohydrate reserves. Branches with reduced carbohydrate reserves may be less likely to survive the dormant season, perhaps because of reduced frost tolerance (Gregory et al. 1987) or because winter respiration exhausts all carbon reserves.

The principal finding of the present study, that riparian cottonwoods are highly vulnerable to drought-induced cavitation, is consistent with the hypothesis that cavitation may contribute to the observed decline of cottonwoods downstream from dams or diversion weirs. The vulnerability of riparian cottonwoods may appear inconsistent with their occurrence in a semiarid region, but it is consistent with their phreatophytic habit. Cottonwoods grow in sandy soil with at least part of the root system always below the water table. The water table closely tracks the level of the river. So cottonwoods rarely experience very negative soil water potentials unlike co-occurring species that may have shallow roots or grow on adjacent higher slopes.

Acknowledgments

We thank John Alexander for measuring shoot resistances of *Populus deltoides* in Vermont. Funds for this work were provided through a cooperative agreement from the USDA Forest Service, Northeastern Forest Experiment Station and a strategic grant from NSERC.

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