

Loss of hydraulic conductivity due to water stress in intact juveniles of *Quercus rubra* and *Populus deltoides*

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Summary

Despite many studies of the percent loss of hydraulic conductivity in excised branches, there is doubt as to whether cutting stems in air introduces unnatural embolism into the xylem at the cut surface. To address this question, hydraulic conductivity was measured in seedlings of northern red oak (*Quercus rubra* L.) and rooted scions of eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) that had been droughted in pots. Results indicate that *in situ* dehydration produced a very similar vulnerability curve (% loss of conductivity versus water potential) to those previously obtained by bench-top dehydration of excised branches of eastern cottonwood and red oak. In eastern cottonwood cuttings, conductivity loss increased sharply below water potentials of -1.0 MPa, with 100% loss of conductivity occurring by -2.0 MPa, whereas conductivity loss in red oak seedlings was more gradual, i.e., increasing below -1.5 MPa and sustaining 100% loss of conductivity by about -4.0 MPa.

Introduction

The use of excised branches is the traditional method for studying drought-induced embolism and loss of conductivity (Crombie et al. 1985, Tyree and Dixon 1986, Sperry et al. 1988a, Cochard and Tyree, 1990). It has never been established whether dehydration of excised stems in air sucks an unnatural amount of air (embolism) into the xylem at the cut end, and if this embolism produces biased data. The vulnerability of some species to drought-induced loss of hydraulic conductivity was unexpectedly high when measured by the traditional methods. Vermont provenances of northern red oak (*Quercus rubra* L.) had 50% loss of hydraulic conductivity when dehydrated to -2.5 MPa, whereas Missouri provenances of the same species experienced predawn stresses of -3.0 MPa during some drought periods (Hinckley and Bruckerhoff 1975, Hinckley et al. 1979). Preliminary studies of eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) found 50% loss of conductivity at water potentials (Ψ) of -1.5 MPa and this seemed unusual because co-occurring species reach this Ψ on a daily basis. These vulnerability data raised concerns about the validity of the traditional techniques.

Accordingly, vulnerability curves were constructed for intact red oak seedlings and rooted eastern cottonwood scions grown and dehydrated in pots and compared with those obtained by bench-top dehydration of excised branches. Results, which are assumed to mimic the natural state more closely than those from excised branch studies, were intended to test the validity of some of the assumptions underlying the

use of bench-top dehydration of excised plant material for studies of drought-induced embolism.

Materials and methods

Seedlings of northern red oak and scions of eastern cottonwood were grown in a greenhouse of the United States Forest Service, Northeastern Forest Experiment Station, South Burlington, Vermont. Oak seedlings were grown for 36 months, including one cold period, in a 1/1 vermiculite/peat potting mix. Cottonwood scions, which came from a single parent, were grown for two months, rooted in a 1/1 peat/perlite mix and potted in a 1/1 vermiculite/peat mix. Other eastern cottonwood stems were excised from coppice material on trees of unknown genetic origin, growing on the campus of the University of Vermont. Plants were brought to the laboratory at the Proctor Maple Research Center, University of Vermont, where this study was conducted.

Each potted plant was exposed to light from a halogen lamp at 350 to 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR at the top of the crown, relative humidity (RH) of $18 \pm 6\%$, and leaf temperature of 25–30 °C. Water potential (Ψ) was measured periodically on excised leaves using a pressure bomb. Oak seedlings were allowed to dry down to a range of –0.5 to –5.0 MPa, whereas eastern cottonwood scions were kept within a range of –0.5 to –2.5 MPa. On reaching the desired Ψ , the plant and pot were put in a black plastic bag, into which several wet paper towels had been placed, and Ψ within the plant and soil were allowed to equilibrate over night so that recently cavitated vessels had more time to become air-filled.

After an equilibration period of about 16 hours, Ψ was measured on at least one leaf to confirm final Ψ . The plant and pot were again put in a plastic bag and placed in a water bath for 3 h to release the tension in the xylem and Ψ was then remeasured. If Ψ was restored to a value of –0.3 MPa, the immersed stem was cut at the base (all cuttings were performed under water). All leaf blades were trimmed off, leaving the petiole and half of the mid-rib intact (Cochard and Tyree 1990). Segments were cut from the upper half of current-year stems, where vessels were shorter and thus easier to work with (Cochard and Tyree 1990). Oak seedlings were sectioned into 6-cm segments and eastern cottonwood scions into 35-cm segments, to insure that about 90% of the vessels in each segment had end-walls intact. The cut ends of each segment were trimmed with a razor blade to remove any crushed tissue, and the segments were placed in a conductivity manifold as described by Sperry et al. (1988a).

Solutions used for conductivity measurements were 10 mol m^{-3} oxalic acid for red oak and 100 mol m^{-3} KCl for eastern cottonwood (oxalic acid, the traditionally used perfusate, and several other solutions caused eastern cottonwood stems to plug), both of which were degassed under vacuum for 1 hour and passed through a 0.2 micron filter. To determine the percent loss of hydraulic conductivity (%LC), these solutions were perfused under moderate pressure (6 kPa for red oak and 10 kPa for eastern cottonwood) through each segment to a Mettler AE 200 electronic balance, which

was linked to a computer for calculation of conductivity (K_h). After measuring an initial conductivity (K_i), segments were subsequently flushed with solution at 170 KPa for 30 minutes to remove existing embolism. Conductivity was remeasured and recorded, and the entire process was repeated until a maximum conductivity (K_{max}) was reached. The %LC was then calculated from $\%LC = 100(K_{max} - K_i)/K_{max}$. Vulnerability curves were generated by graphing %LC versus the lowest (most negative) Ψ attained by the plant.

Stems of the same parent material as that used in the intact seedling measurements were cut in air. Some additional eastern cottonwood stems were collected from coppice material of unknown genetic origin. The excised stems were then dehydrated on the bench top and, on reaching a desired Ψ , were placed in a bag which was wrapped with wet paper towels, and in turn placed in another plastic bag. The Ψ in these stems was allowed to equilibrate for about 16 hours, at which time Ψ was measured. Plants were covered again and the cut ends placed in water and recut to break the tension in the xylem. After about 1 hour of rehydration, Ψ was measured to verify that it had been restored to -0.3 MPa. From this point on, these stems received the same treatment as the intact stems described above.

Results and discussion

Cottonwood stems of whole, rooted eastern cottonwood scions experienced a sharp increase in loss of conductivity due to embolism at water potentials below -1.0 MPa. Loss of conductivity rapidly rose to 100% at $\Psi = -2.0$ MPa. These data are similar to those involving dehydration of excised stems cut from rooted scions and coppice material (Figure 1).

Oak seedlings used here yielded a similar vulnerability curve to that found by

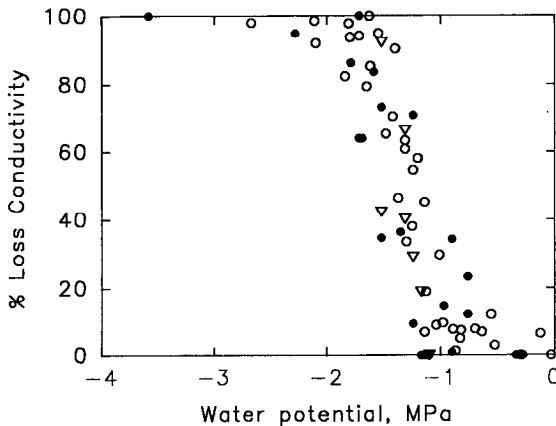


Figure 1. Vulnerability curve for eastern cottonwood measured on excised branches dehydrated after excision on coppice material (O), on branches excised from rooted scions (∇), and on rooted scions dehydrated in pots (\bullet). Xylem tensions in potted plants were released by watering the pots before cutting segments for measurement of percent loss of conductivity.

Cochard and Tyree (1990), with loss of conductivity increasing from 10% at -1.5 MPa to 100% at about -4.0 MPa (Figure 2).

In situ dehydration of potted red oak and eastern cottonwood plants produced similar losses in hydraulic conductivity to that of excised stems of the same species dehydrated to the same range of Ψ . In eastern cottonwood there appeared to be more variability in the scatter of points for the vulnerability curve of rooted scions than for the excised stems of the same scions or from the coppice material of unknown genetic origin. The reason for this is not known.

If cavitations are air-seeded by air bubbles sucked into water-filled vessels adjacent to already embolized vessels (Crombie et al. 1985, Sperry et al. 1988b, Sperry and Tyree 1989, Sperry and Tyree 1990), it is likely that many cavitation events are induced by air bubbles sucked in from the base of excised stems. Perhaps this accounts for the reduced variability in Figure 1 (open symbols versus closed circles). Air seeding from the distal ends of intact (and excised) branches is probably initiated from vessels opened by leaf or stem damage, e.g., herbivory and wind damage. The higher variability in the vulnerability curves of rooted plants might be accounted for if we assume that there are regions of vessels with high vulnerability separated axially by vessel regions of low vulnerability. High vulnerability regions without at least one embolized vessel could not be embolized until embolisms have progressed through the connecting low vulnerability region, which would require lower Ψ than if the high vulnerability region had a prior embolism. If embolized vessels from distal portions are more common and more widely distributed in some individuals than in others, then the variability at the initial state might account for the variability in response to water stress. The factor that accounts for the vulnerability of vessels to air-seeding is the porosity of the pit membranes. The similarity of the vulnerability data of rooted plants and excised branches suggests that pit membranes in damaged

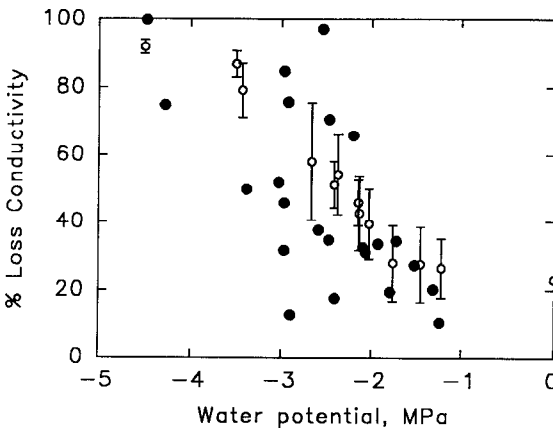


Figure 2. Vulnerability curve for red oak measured on seedlings dehydrated in pots (●) and on excised branches from mature trees dehydrated after excision (○). Xylem tensions in potted plants were released by watering the pots before cutting segments for measurement of percent loss of conductivity. The latter data are replotted from Cochard and Tyree (1990). The error bars are standard deviations ($n = 8$ to 10).

leaves or proximal portions of stems are about as porous as in the cut base of stems.

Eastern cottonwood is the most vulnerable temperate species to cavitation events reported so far, although some tropical trees have similar vulnerabilities (Tyree et al. 1991). The high vulnerability to xylem dysfunction caused by drought in eastern cottonwood probably explains why this species is confined to riparian habitats. More work is needed to determine if vulnerability to cavitation is the main factor limiting the distribution of eastern cottonwood among different habitats.

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