

Xylem cavitation and loss of hydraulic conductance in western hemlock following planting

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Summary Following planting, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) seedlings experience water stress and declining xylem pressure potential (Ψ_x). Low Ψ_x can result in xylem cavitation and embolism formation, causing a decline in hydraulic conductance. This study focused on the relationship between Ψ_x , xylem cavitation and transpiration (E) of newly planted seedlings. Leaf specific hydraulic conductance (k_{AB}) declined from 0.56 to 0.09 mmol m⁻² s⁻¹ MPa⁻¹ over a 9-day period. Stomatal conductance (g_s) declined from 143.5 to 39.15 mmol m⁻² s⁻¹ over the same period without an associated change in environmental conditions. A vulnerability profile indicated a 30% loss in hydraulic conductivity when seedlings experienced a Ψ_x between -2.5 and -3.0 MPa. A Ψ_x of -4.0 MPa led to a complete loss of conductivity. We conclude that following planting, western hemlock seedlings often experience Ψ_x values that are low enough to cause xylem cavitation and a decline in k_{AB} .

Keywords: transpiration, *Tsuga heterophylla*, water stress vulnerability.

Introduction

Newly planted tree seedlings frequently experience water stress because of poor root–soil contact (Sands 1984, Grossnickle 1988), a reduction in the number of unsubsized roots (Johnson et al. 1988), low soil temperatures (Running and Reid 1980, Lopushinsky and Kaufmann 1984), root breakage and root damage caused by desiccation. If, for any or all of these reasons, water uptake is less than transpirational water loss, xylem pressure potential (Ψ_x) will decline.

Declining Ψ_x can result in cavitation in xylem elements, thereby causing a reduction in xylem hydraulic conductance (Borghetti et al. 1989, Tyree and Sperry 1989), which in turn, may lead to a further decline in Ψ_x . Depending on the severity of xylem cavitation, the resulting decline in Ψ_x can lead to a reduction in stomatal conductance (Pena and Grace 1986, Borghetti et al. 1989), foliage or branch loss (Zimmermann 1983), or plant mortality (Tyree and Sperry 1988).

Changes in the hydraulic conductance of western hemlock seedlings (*Tsuga heterophylla* (Raf.) Sarg.) following planting

and the resultant effect on post-planting water relations have not been well characterized. We evaluated leaf specific hydraulic conductance (k_{AB}), of planted western hemlock seedlings. Following field measurements, we constructed a vulnerability profile (Tyree and Sperry 1989) in the laboratory to link recorded water stress with associated losses in hydraulic conductivity (k_h) caused by xylem cavitation. Examining both the calculated reduction in k_{AB} and the vulnerability profile allowed evaluation of the effects of water stress on western hemlock seedlings during planting and establishment.

Methods

Leaf specific hydraulic conductance

Plant material All seedlings were obtained from Oregon Coast Range sources and grown in local nurseries as bareroot or container-grown stock. Bareroot stock, which had been grown for 1 year in a container and 1 year in a nursery bed, was obtained from the Industrial Forestry Association (IFA) Nursery in Canby, OR. Large, three-year-old container-grown stock was obtained from the Environmental Protection Agency in Corvallis. One-year-old container-grown stock was grown at the Champion International Nursery in Lebanon. Root pruning treatments were applied as follows: (1) bareroot stock, unpruned; (2) bareroot stock, root pruned to 20 cm; (3) bareroot stock, root pruned to 10 cm; (4) 3-year-old container-grown stock, undisturbed root system; and (5) 1-year-old container-grown stock, undisturbed root system. Root pruning treatment effects were not statistically significant, so root pruning treatments within a stock type were combined for subsequent analyses.

Site The planting site (44°30' N, 123°30' W) was located on a northeast-facing slope in Oregon's central Coast Range, approximately 5 km northeast of Eddyville. The site, which had been clearcut and burned the preceding fall, was practically devoid of aboveground vegetation at the time of planting. Ninety seedlings per root treatment were planted on March 8, 1990, in a randomized design with 0.6 × 0.6 m spacing. It rained steadily while the trees were being planted and the soil was fully saturated. The temperature was about 10 °C.

Measurements Leaf specific hydraulic conductance (k_{AB}), was obtained by dividing transpiration rate (E), measured with a null-balance porometer, by leaf–soil water potential difference ($\Delta\Psi$) (Beardsell et al. 1972, Roberts and Knorr 1977, Running and Reid 1980, and Mattson-Djos 1984), which was estimated from shoot xylem pressure potential (Ψ_x) on the assumption that soil water potential was close to zero. Measurements of Ψ_x were made with a pressure chamber (PMS Instrument Co., Corvallis, OR).

Fifteen intact seedlings (three per treatment) were measured on each sample date. Measurements of k_{AB} began on Day 4 after planting, when the foliage was dry enough for porometer measurements to be made, and continued on every third day or as soon as weather conditions permitted.

Predawn xylem pressure potential (Ψ_{pd}) was measured with a pressure chamber between 0400 and 0430 h. Transpiration (E) and g_s were measured on intact needles between 0800 and 1000 h (depending on when the foliage dried) with a steady state porometer (Model LI-1600, Li-Cor, Lincoln, NE). Needles contained in the porometer cuvette during measurements were removed, placed in a plastic bag, labeled, and returned to the laboratory, where projected leaf area was measured with a leaf area meter (Model LI-3100, Li-Cor). Simultaneous measurements of temperature and relative humidity were used to compute water vapor pressure deficit (VPD). The Ψ_x of a nearby detached stem was measured at the time g_s was measured. Measurements of E and g_s were divided by the leaf area in the cuvette to obtain area-based rates.

Vulnerability profile

Measurements of seedling cavitation and xylem pressure potential Bareroot western hemlock seedlings were held temporarily in cold storage and then moved to a growth room where they were allowed to desiccate. A sample seedling was prepared by severing the root system at the root collar, removing a 5-cm-long stem segment from the base of the seedling, and placing it in water for measurement of initial hydraulic conductivity (k_h). The newly exposed base of the seedling was immediately sealed with paraffin wax to prevent localized desiccation. To monitor cavitation events on the seedling, an R15 transducer (Physical Acoustic Corp., Princeton, NJ) was attached to a 1-cm² patch of xylem, which was exposed by carefully removing the bark and phloem approximately half-way between the tip and the base of the seedling. The transducer was connected to an acoustic detector, the 4615 Drought Stress Monitor (Physical Acoustic Corp.). Total amplification of the signal was 80 dB. The exposed xylem was covered with petroleum jelly to prevent local desiccation and improve signal transmission. Following initiation of cavitation, a second 5-cm stem segment was removed from the base of the seedling. The newly cut end of the seedling was sealed with paraffin wax. The detached segment was immediately placed in water and used to measure k_h . At the same time, measurements of Ψ_x were made on a small foliar sample in a pressure chamber apparatus.

A third segment and sometimes a fourth (depending on seedling size) was sampled, and Ψ_x measured, as desiccation

progressed. This procedure was repeated with 10 seedlings, with each seedling providing three to four segments for k_h and xylem pressure potential measurements.

Measurements of hydraulic conductivity of stem segments

Hydraulic conductivity (k_h) was measured by the method of Sperry et al. (1987) as modified by Lo Gullo and Salleo (1991). To check for leaks in the tubing and to confirm cavitation, each segment was perfused, under 10 kPa of pressure, with 0.2% (w/v) safranin dye (filtered to 0.22 μ m). Any seedling showing signs of cavitation before the desiccation treatment (i.e., as determined by perfusion of the first segment to be sampled) was eliminated from the population used in constructing the vulnerability curve.

For measurements of k_h , the excised stem segment was submerged under water, the bark removed, and 1 cm trimmed from the segment ends to eliminate air-filled tracheids (Zimmerman 1983). While still submerged, the proximal end of the stem section was securely attached to tubing containing a solution of 10 μ mol l⁻¹ oxalic acid prepared with deionized distilled water, filtered to 0.22 μ m and degassed by sparging with helium. The solution in the tubing was pressurized to 10 kPa by gravity.

The amount of solution passing through the stem segment was measured by attaching a pre-weighed vial containing filter paper to the distal end of the segment. The vial was removed and weighed at 60-s intervals.

Calculations Hydraulic conductivity of each segment was calculated by the equation:

$$F = k_h \left(\frac{dP}{dx} \right),$$

where F is the measured flow rate, dP is the pressure differential across the segment (10 kPa), and dx is the segment length. To compare segments with varying diameters, the specific hydraulic conductivity, k_s , of each segment was calculated by dividing k_h by the cross-sectional area of that segment. To ensure that k_s was uniform throughout the length of the sampled stem, the stems of three seedlings were dissected, before cavitation, into four adjacent segments, and k_s measured on each.

Percent loss in k_s was calculated by:

$$\text{Percent loss} = \left(\frac{k_{si} - k_{\Psi}}{k_{si}} \right) 100,$$

where k_{si} is initial specific conductivity before cavitation and k_{Ψ} is the specific conductivity at a given value of Ψ_x . To construct the vulnerability profile, percent loss was plotted against Ψ_x measured at the time of segment removal.

Results

Leaf specific hydraulic conductance

Predawn xylem pressure potential averaged -0.5 MPa and did not vary significantly during the experiment except on Day 16,

when the average value ($n = 15$) was -1.9 MPa (Figure 1). On this day, at 0400 h, there was an east wind and no dew on the foliage. The low Ψ_{pd} values were the result of predawn transpiration and did not accurately reflect soil water potential.

Mean midmorning Ψ_x varied during the measurement period (Figure 2). Initially, values declined rapidly, but, by 30 days after planting, Ψ_x recovered to slightly below the measurements made on Day 4. There was variability among seedlings within each measurement period, with certain samples experiencing episodes of extremely negative Ψ_x . The return of favorable mean Ψ_x did not result in an increase in g_s (Table 1).

Leaf specific hydraulic conductance (k_{AB}) declined sharply in the first 11 days following planting (Figure 3), primarily as a function of decreasing g_s , which remained low throughout the experiment even when Ψ_x increased (Table 1).

As illustrated in Figure 4, VPD varied between 0.47 and 1.3 kPa; and g_s ranged from 22 to 139 $\text{mmol m}^{-2} \text{s}^{-1}$. There was no relationship between VPD and g_s after Day 13, when the stomata ceased to be responsive to changes in VPD (Figure 4).

Vulnerability profile

Specific hydraulic conductivity did not vary significantly between adjacent segments on a non-cavitated seedling, indicat-

ing that the first basal segment could be used to measure the initial (or non-cavitated) k_{si} needed to calculate percent loss in hydraulic conductivity.

Vulnerability to cavitation for coastal western hemlock seedlings is illustrated in Figure 5, where percent loss in k_s is plotted against Ψ_x . When Ψ_x dropped to between -2.5 and -3.0 MPa, k_s loss was 30%. When Ψ_x was below -3.0 MPa, k_s loss was 50%, and when Ψ_x fell to -4.0 MPa, conductivity approached zero. The relative steepness of the vulnerability profile illustrates the rapid onset of xylem cavitation and subsequent loss of k_s following exposure to low Ψ_x .

Discussion

A reduction in leaf specific hydraulic conductance (k_{AB}) occurred in western hemlock seedlings after planting. Stomatal aperture was limited by the ability of the hydraulic system to meet transpirational demand, and remained low even after more than 60 days. Omi et al. (1991) observed recovery in g_s of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) bareroot seedlings transplanted to a hydroponic system following the onset of root growth. In transplanted western hemlock seed-

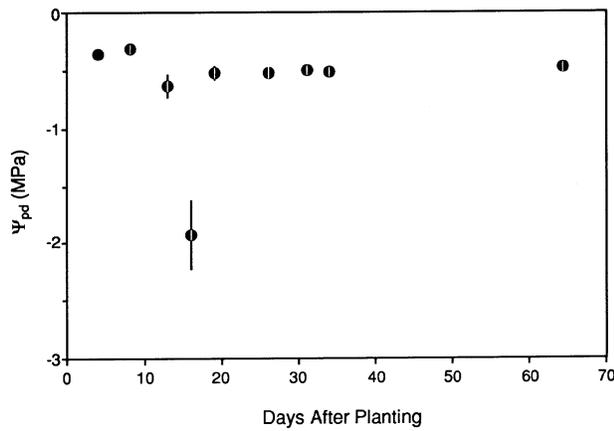


Figure 1. Predawn xylem pressure potential (Ψ_{pd}) of western hemlock seedlings following planting. Each point is the mean of 15 values. Vertical bars represent the standard error of the mean.

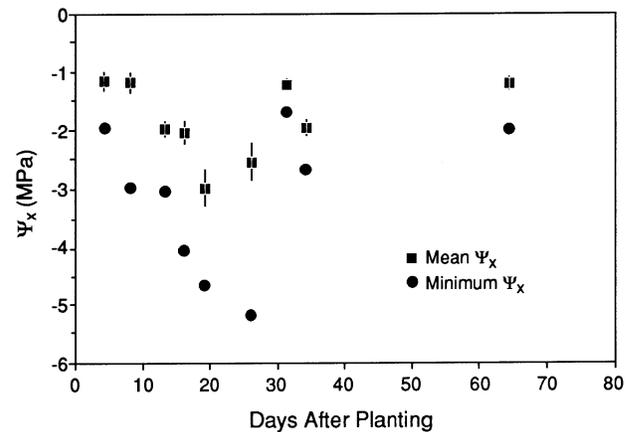


Figure 2. Midmorning mean and minimum xylem pressure potentials (Ψ_x) of western hemlock seedlings following planting. Measurements were taken at the same time g_s was measured. Vertical bars represent the standard error of the mean ($n = 15$).

Table 1. Calculations of hydraulic conductance (k_{AB}) and field measurements of stomatal conductance (g_s), midmorning xylem pressure (Ψ_x), transpiration (E), and vapor pressure (VPD) on western hemlock following planting. Standard errors are in parentheses; $n = 15$.

Days following planting	Mean k_{AB} ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)	Mean g_s ($\text{mmol m}^{-2} \text{s}^{-1}$)	Mean Ψ_x (MPa)	Mean E ($\text{mmol m}^{-2} \text{s}^{-1}$)	VPD (kPa)
4	0.54 (0.08)	143.5 (26.1)	-1.17 (0.11)	0.63 (0.07)	0.48
8	0.29 (0.04)	25.2 (3.5)	-1.13 (0.17)	0.30 (0.04)	1.32
13	0.09 (0.02)	39.2 (8.7)	-1.98 (0.12)	0.17 (0.04)	0.50
16	0.11 (0.01)	43.5 (4.3)	-2.06 (0.17)	0.21 (0.03)	0.51
19	0.09 (0.01)	27.8 (3.5)	-3.30 (0.53)	0.26 (0.03)	0.99
26	0.11 (0.01)	24.4 (1.7)	-2.64 (0.22)	0.24 (0.02)	0.79
30	0.10 (0.01)	21.7 (2.2)	-1.23 (0.07)	0.12 (0.01)	0.47
34	0.12 (0.01)	16.1 (1.7)	-1.97 (0.03)	0.24 (0.03)	1.27
64	0.15 (0.02)	21.7 (2.2)	-1.20 (0.09)	0.17 (0.01)	0.51

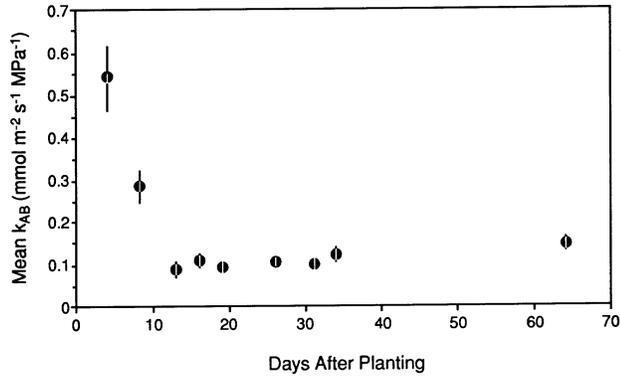


Figure 3. Mean leaf specific hydraulic conductance (k_{AB}) for western hemlock seedlings following planting. Values represent means ($n = 15$); vertical bars represent standard errors of the mean.

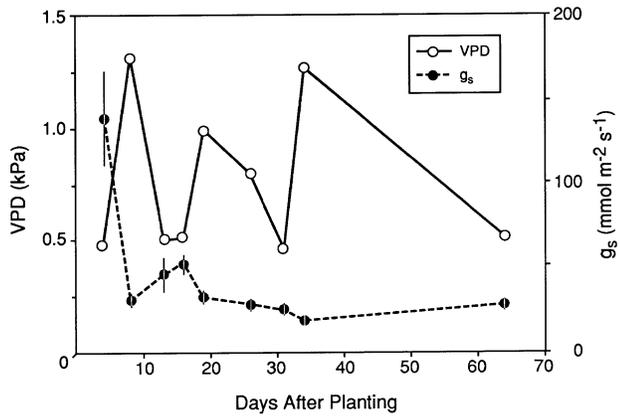


Figure 4. Mean vapor pressure deficit (VPD) and stomatal conductance (g_s) following planting of western hemlock seedlings. Both measurements were taken at the same time in midmorning after the foliage had completely dried (0800–1000 h). For g_s , bars represent standard error of the mean ($n = 15$).

lings, however, we saw no evidence of increasing k_{AB} following the onset of root growth.

A decline in g_s of newly planted western hemlock is not a function of environmental conditions. Table 1 shows that an initial Ψ_x of -1.17 MPa was sufficient to maintain a sap flux of $0.63 \text{ mmol m}^{-2} \text{ s}^{-1}$. However, after 2 weeks, during which there was no significant change in Ψ_{pd} , Ψ_x had declined to -2.06 MPa, but sap flux was only $0.21 \text{ mmol m}^{-2} \text{ s}^{-1}$ (Figure 1). In almost all cases illustrated in Table 1, the VPD was well below the value of 1.0 kPa at which Marshall and Waring (1984) demonstrated stomatal closure in western hemlock. The value of k_{AB} was severely reduced, resulting in a more negative Ψ_x and earlier diurnal stomatal closure, even when soil water content was high.

Borghetti et al. (1989) recorded a similar phenomenon in *Picea abies* (L.) Karst. following water stress and xylem cavitation. Even after rewatering, E and g_s were lower for cavitated seedlings than for non-cavitated controls at the same Ψ_x . Simi-

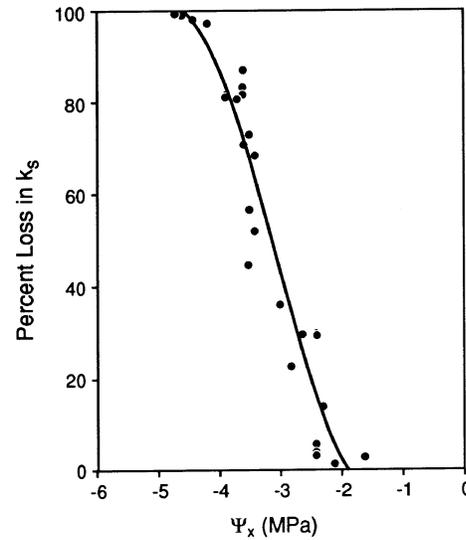


Figure 5. Vulnerability profile for western hemlock seedlings: percent loss in specific conductivity (k_s) versus xylem pressure potential (Ψ_x). Each point represents one k_s and Ψ_x measurement. The line represents a fitted logistic regression of the data ($P < 0.0001$).

larly, transpiration rates of *Pinus sylvestris* L. following xylem cavitation remained below those of non-cavitated controls even though the treatments were measured at similar values of Ψ_x (Pena and Grace 1986). Sperry et al. (1993) found a similar increase in Ψ_x in birch when they induced xylem cavitation. In all of these examples, xylem cavitation was implicated in a reduction of k_{AB} , which resulted in a decreased Ψ_x for a given rate of E , or a reduced rate of E for a given value of Ψ_x .

The vulnerability profile for western hemlock seedlings (Figure 5) illustrates a low tolerance to water stress. An effect of xylem cavitation on k_s was evident. For example, when Ψ_x was -2.5 MPa, there was a loss of almost 20% in k_s . The relative steepness of the curve illustrates a rapid escalation of cavitation-induced loss in conductivity, giving the seedling a narrow window (-1 to -2.5 MPa) in which to make adjustments to, and reduce impacts of, water stress. Tyree and Dixon (1986) constructed a vulnerability profile for *Tsuga canadensis* (L.) Carr. with similar results; cavitation was initiated at -2.5 MPa and rapidly escalated, with 100% loss of k_s at -4.0 MPa.

In nature, the vulnerability of a species to cavitation tends to correlate with xylem tensions, and xylem pressure potential is rarely so negative that cavitation occurs (Sperry and Tyree 1990). In this experiment, western hemlock seedlings were unable to maintain sufficient stomatal control over Ψ_x to prevent cavitation (Figures 2 and 5).

Even after experiencing Ψ_x sufficiently low to cause xylem cavitation, surprisingly few seedlings died. However, seedlings suffered needle loss and branch mortality. Tyree and Sperry's (1988) "runaway cavitation" model illustrates that cavitation-induced mortality can be halted either through stomatal closure or a reduction in leaf area. This supports an earlier model proposed by Zimmermann (1983) that suggests

that plants are hydraulically designed to sacrifice minor branches and individual needles to maintain the irreplaceable main stem. In addition, both models predict that during periods of dynamic water stress, cavitation is most likely to occur in xylem tissue where the resistance to water flow is the highest. Resistance to water flow is much higher in stems than in roots, particularly at branch junctions, making stems the most probable locations for embolisms to form.

Vulnerability curves have been developed for numerous tree species, and there is a correspondence between drought tolerance and the ability to conduct water following exposure to low Ψ_x (Tyree and Ewers 1991). Of several coniferous species examined, *Juniperus virginiana* L. was found to be least vulnerable, with only a 20% loss of k_s at -5.0 to -6.0 MPa, whereas *Abies balsamea* (L.) Mill. experienced a 50% loss at -2.0 to -3.0 MPa (Tyree and Ewers 1991). Cochard (1992) obtained similar results for a variety of coniferous species. The more drought-tolerant species, such as *Cedrus atlantica* Manetti, were the most resistant to cavitation, and the more drought-intolerant *Pinus sylvestris*, the least resistant.

There is little information on the ability of Pacific Northwest conifer species to avoid xylem cavitation. Cochard (1992) developed a vulnerability profile for branches of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) growing in France. Reduction in k_s began at 3.0 MPa, with a 50% loss by -3.6 MPa and total loss occurring by -5.0 MPa. Western hemlock was more vulnerable than Douglas-fir, with cavitation and subsequent loss in k_s starting at a less negative value of Ψ_x . These results agree with the distributions of these species in the Pacific Northwest. Western hemlock has a more limited distribution than Douglas-fir, with populations found on wetter coastal and upper Cascade Range sites (Franklin and Dyrness 1973).

We conclude that, following planting, western hemlock seedlings experience water stress attributable to the limited water uptake capacity of the root system. Such water stress can be sufficient to cause xylem cavitation and embolism formation. The embolized tracheids cause a decline in leaf specific hydraulic conductance, which leads to a reduction in stomatal conductance, defoliation, or death.

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