Xylem Cavitation: An Indication of Moisture Stress in Newly Planted Western Hemlock Seedlings[1]

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Abstract.--Xylem cavitation occurs when water potentials reach a level great enough to introduce air into the water conducting system. Cavitation events in western hemlock were found to begin at -1.9MPa and reach very high levels at -3.4MPa. The best place to monitor cavitation events was the base of the seedling stem.

INTRODUCTION

Water molecules in xylem conduits are under tension and following increasing moisture stress a large number of hydrogen bonds can break leaving a void filled with water vapor. This phenomena is commonly referred to as cavitation. Cavitation leads to the further introduction of air, which comes out of the surrounding tissues, forming an embolism restricting water transport (Tyree and Sperry, 1988).

Breakage of the water column results in an acoustic emission (AE) which can be detected in both low (Milburn and Johnson, 1966) and ultrasonic (Tyree and Dixon 1983, Tyree et al 1984) frequencies. Detection on the ultrasonic frequency is preferred due the lack of background noise interference and the ability to make more than one measurement on the same plant concurrently.

Results reported in the literature have established a clear relationship between cavitation events and AE frequency. Tyree and Dixon (1983) found AE occurred in *Thuja occidentalis* only when water potentials exceeded -1mPa and the rate of AEs increased as xylem pressure became more negative. AEs were found to stop following rewetting and a ~~less negative value o~~f xylem pressure potential. Loss in hydraulic conductance was related to the initiation of AEs in *Thuja, Tsuga* and *Acer* (Tyree and Dixon 1986). It was also found that the last vestiges of hydraulic conductance in conifers corresponded to the cessation of AEs. The cumulative number of AEs has been found to correspond to the number of tracheids in small samples of Thuja (Tyree et al 1984) . Although Sandford and Grace (1985), using a less efficient AE counting system, found only 16% of the expected AEs from a sample of *Chamaecyparis* wood.

Many of the initial studies have involved the used of detached woody stems which are debarked then dehydrated and rehydrated rapidly under laboratory conditions. More recent applications have involved the use of whole plants under controlled environmental conditions. Jones et al (1989) utilized AE monitoring equipment to quantify the relationship between apple root stock variety and the initiation and severity of embolism formation during water stress. A 70% reduction in hydraulic conductance was found in intact potted *Picea abies* seedlings due to embolism formation following 3 drought stress periods (Borghetti et al, 1989). They also showed that the effect of the embolism formation was cumulative and the plants did not recover fully even following rewatering.

BACKGROUND

Survival rates of western hemlock *(Tsuga heterophylla)* following planting are inconsistent and unreliable. A research project was undertaken to explain

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the drought symptoms often associated with the death of hemlock even when soil moisture is not limiting. The research has focused on the ability of the root system to provide water to the foliage by monitoring plant water conductance since it is impossible to make a direct measurement of root conductivity on intact seedlings. Total conductance from the soil to the needle can be measured however and the relative change in total conductivity should indicate treatment effects.

Water potential (**?**), stomatal conductance and transpiration measurements were made immediately following planting and every third day for 6 weeks on 3 hemlock seedlings from each of 5 different root treatments, for a total of 15 trees per sample date. Results indicated that poor root conductivity creates severe water stress following planting even in moist soils. Particularly in seedlings with pruned suberized roots.

As with any experiment unexplained observations often lead to more questions and further exploration. The predawn water potential data obtained on the fourth sample date raised some interesting questions. Throughout the experiment, with the exception of sample 4, predawn water potentials averaged -0.5MPa across all treatments. On sample date #4 predawn water potentials averaged -l.9MPa ,with a range of -1.2 to -4.0 MPa, across all treatments, with no extreme climatic conditions except for the lack of dew on the foliage and a dry east wind. The inability of the seedlings to recover during the preceding night was severely hampered by either a lack of stomatal closure or the formation of embolisms inhibiting water conductance to the fine branches which were being sampled. Tyree and Sperry (1988) indicated that embolisms occur more frequently in minor branches than in major branches.

In the days following this occurrence of high water potentials, foliar die-back and mortality was noted on several individuals which correlated with the treatments having the highest predawn measurements. Another phenomena of interest that occurred on this sample date was the recovery noted in the 9:00 AM readings on the same group of seedlings. Xylem water potential actually became less negative on some seedlings, indicating an increased availability of water which can occur following cavitation (Borghetti et al, 1989)

The results of this experiment coupled with observations of foliar die-back and seedling mortality indicate that newly planted western hemlock experience water deficits great enough to cause cavitation and exhibit symptoms consistent with the cavitation model. An experiment was designed to determine: 1. The best location on the seedling to monitor for cavitation. 2. the **?** at which cavitation occurs in western hemlock seedlings.

METHODS

Western hemlock plug-l seedlings were obtained from the Industrial Forestry Association (IFA) Nursery. The seedlings were donated by Starker Forests Inc. Corvallis, Oregon.

Three seedlings were removed from cold storage and planted in the same pot using potting soil, vermiculite and perlite (2/1/1). The seedlings were then placed in a greenhouse maintained at a day/night temperature of 28/20°C. Light levels averaged 700umol with a range of 300-l200umol. The pot was watered to field capacity. The water potential the seedling experienced was not a result of water availability but from growing in an environment with a high vapor pressure deficit putting an increased stress on the water conducting system.

One hour following planting an ultrasonic detector (Drought Stress Monitor, Model 4615 Physical Acoustic Corporation, Princeton, NJ **)** was attached to an individual seedling via six acoustic sensors. Three sensors were placed on the main stem of the seedling (low, mid, and high levels) and three sensors were placed on lateral branches (low, mid and high laterals). The sensors were attached following removal of a small patch of bark and phloem exposing the xylem. The wound was covered with ultrasonic jelly to inhibit desiccation and improve transmission of the signal. The sensor was then clamped firmly to the stem in direct contact with the xylem.

A programmable interface was used to switch between the six sensors every minute, 24 hours a day so data was collected for one minute out of six per sensor. The data was stored in the Drought Stress Monitor and later downloaded into a PC for further analysis

On the second day of the experiment **?** measurements were made on the seedling being monitored for acoustic emissions. Measurements were made at 4:15, 9:00, 11:00, 12:00, 13:00, 15:00, and 17:00. All **?** measurements were made with a pressure chamber apparatus (PMS Instruments, Corvallis, Or.).

RESULTS

The acoustic sensor placed at the base of the seedling stem recorded at least five times more acoustic emissions than any other sensor throughout the day (table 1).

Table 1.--Number of acoustic emissions recorded over a 9 hour period by six sensors placed on a single plug-1 western hemlock seedling.

Time	Seedling stem			Lateral branch		
	low	mid	top	low	mid	top
(hour)	--------*AE per minute*[1]--------					
8:00	0	0	0	0	0	0
9:00	57	7	8	1	1	0
10:00	253	17	31	4	3	0
11:00	246	33	62	9	4	1
12:00	407	46	84	17	6	2
13:00	479	40	86	7	7	2
14:00	172	18	34	9	3	1
15:00	135	9	30	2	2	1
16:00	30	6	13	1	0	0
17:00	0	0	0	0	0	0

[1] Acoustic emissions per minute were averaged over the one hour period.

Predawn water potential was -1.2 MPa. The number of acoustic emissions recorded by the drought stress monitor increased as **?** became more negative with a decrease in acoustic emissions in the afternoon as **?** became less negative (Fig. 1) . Acoustic emissions began at -1.9MPa reaching a peak at -3.4MPa when **?** began to increase.

DISCUSSION

Acoustic emissions were higher at the base of the seedling for a variety of reasons. The larger stem diameter increased the contact area with the sensor allowing for more signals to be recorded. An increased diameter also increases the number of tracheids to be close enough to the sensor to transmit a signal. The most notable reason has to do with tracheid size however.

Logullo and Salleo (1991) demonstrated that the vulnerability of a

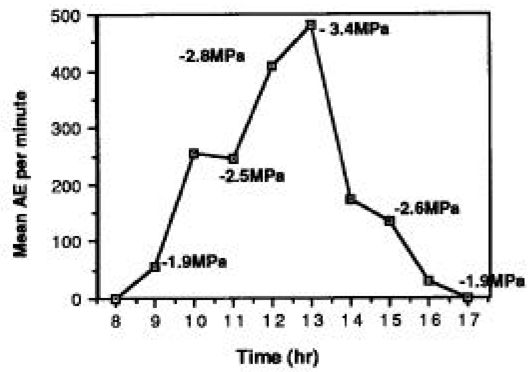

Figure 1.--Acoustic emissions per minute (averaged over one hour). Data was obtained from a single sensor placed at the base of a plug-1 western hemlock seedling. Ψ measurements are printed alongside the appropriate times.

xylem tracheid to embolism was a direct function of diameter. The larger diameter conduits were found to be more prone to embolism in *Ceratonia siliqua* L. Since larger tracheids are found at the base of the trunk it is not surprising that these are the first to cavitate in western hemlock seedlings.

The loss of these large tracheids due to cavitation may have a significant effect on water conductivity since the relationship between hydraulic conductivity and conduit diameter is so strong. Zimmerman (1984) pointed out that flow rate is proportional to the 4^{th} power of the radius of the capillary. If a capillary has a diameter of 1 it has a relative flow rate of 1 and a capillary with a diameter of 4 has a relative flow rate of 256. The loss of these larger conduits under relatively high **?** (-1.9MPa) may have a significant effect on the ability of the seedling to conduct water to the foliage.

The rate of cavitation was found to be relatively high at -2.5MPa, which is not an unusual **?** to find in newly planted western hemlock seedlings. Sufficiently negative water potentials for significant cavitation were found to occur frequently by 9:00am on sunny days 13-19 days following planting in moist soils.

Following a cavitation episode the seedling must make an adjustment to the new hydraulic conditions. This adjustment may come in the form of a foliar loss, particularly of lower lateral branches and/or a reduction in current years growth. If the seedling is unable to make such adjustments then the **?** may reach a level where cavitation is rampant resulting in seedling mortality.

SUMMARY

It has been known for many years that newly planted seedlings experience episodes of moisture stress prior to full establishment. The subsequent results of these episodes on seedling physiology has not been fully explored however. Long term effects on the water conducting system due to cavitation may carry over into the following growing season. Further exploration into this topic is now underway looking at the ability of the western hemlock seedling to refill cavitated tracheids and the relationship between cavitation and loss of hydraulic conductivity.

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