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Cavitation Events in *Thuja occidentalis* L.?[1]

UTRASONIC ACOUSTIC EMISSIONS FROM THE SAPWOOD CAN BE MEASURED

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ABSTRACT

Ultrasonic acoustic emissions (AE) in the frequency range of 0.1 to 1 megahertz appear to originate in the sapwood of *Thuja occidentalis* L. The AE are vibrations of an impulsive nature. The vibrations can be transduced to a voltage waveform and amplified. The vibrations of each AE event begin at a large amplitude which decays over 20 to 100 microseconds. Strong circumstantial evidence indicates that the ultrasonic AE result from cavitation events because: (a) they occur only when the xylem pressure potential Ψ_{xp} is more negative than a threshold level of about −1 megapascal; (b) the rate of AE events increases as Ψ_{xp} decreases and when the net rate of water loss increases; (c) the AE can be stopped by raising Ψ_{xp} above −1 megapascal. Ultrasonic AE have been measured in whole terminal shoots allowed to dry in the laboratory, in isolated pieces of sapwood as they dried in the laboratory, and in whole terminal shoots in a pressure bomb when Ψ_{xp} was decreased by lowering the gas pressure in the pressure bomb.

Ever since the introduction of the cohesion theory of sap ascent in plants, it has been recognized that water in xylem conduits can be under tension (= minus Ψ_{xp}[2]). The maximum tensions in the xylem water of most plants are typically 1 or 2 MPa (rarely 10 MPa). Xylem water under tension is in a metastable state so a cavitation can occur, *i.e.* a large number of hydrogen bonds can break near one locus to leave a void filled with only water vapor. Renner (12) first observed cavitations in the annulus cells of fern sporangia and estimated that cavitations occur when tensions reach 30 to 50 MPa. Evidence concerning tensions at which cavitation events can occur in xylem conduits is conflicting.

AE accompany cavitations in water-filled glass capillary tubes (3). It has been demonstrated that AE can be detected with a modified microphone and amplified with audio amplifiers (7, 8, 10). In *Ricinus*, AE in the frequency range of 0.2 to 2 kHz have been studied. They last a few ms and appear to be associated with cavitation events; the AE start at tensions as low as 0.5 MPa and are frequent at 1 MPa (9).

Cavitations are generally thought to be detrimental to the water economy of plants and especially trees. For example, if a cavitation occurs in the tracheid of a conifer, the void will expand to fill the entire lumen of the tracheid. Although the void/water interface is probably prevented from advancing into adjacent tracheids by the valve action of the tori in bordered pits, the cavitated tracheid is rendered nonfunctional. If a substantial fraction of the available tracheids cavitate, then a significant constriction of water flow (4) to leaves will result and physiologically detrimental water stresses will arise.

No serious attempt has been made to measure AE in the stems of trees. Since cavitation may explain seasonal changes in sapwood water content, then AE could be associated with this phenomenon. In numerous conifers, the volume of water in the sapwood changes annually by 40 to 50% being maximum in early spring and minimum in late summer (17). This decline in water volume is accompanied by an equal increase in void volume. These voids are probably initiated by cavitations because they occur most frequently when tensions are largest, *i.e.* when Ψ_{xp} is most negative. The volume of water removed from the sapwood of trees can be a significant fraction (10–50%) of the annual volume of evaporation in some forest stands (15, 17). This seems to indicate an adaptive strategy of trees to tap the rather large water reserves in their necessarily massive stems and thereby reducing demands on soil water when transpiration rates are high; therefore, limited numbers of cavitations may be of some benefit to trees.

To date cavitation studies have relied on measuring AE in the audio frequency range, usually 0.2 to 2 kHz. This drastically restricted mechanical manipulation since ambient noise is registered as AE. It is usually necessary to isolate the plant in a soundproof chamber and the plant can not be touched during measurement without creating spurious AE.

We guessed that cavitation events might have a component of AE in the ultrasonic frequency range. Detecting cavitations through ultrasonic AE would have at least one major advantage; audio frequency range laboratory noise generated by people, instruments, and manipulation of the plant material could be filtered out by employing high pass electronic filters and by using sound transducers that respond primarily in the higher frequency range. Our guess proved to be correct, and in this paper we report our initial findings.

MATERIALS AND METHODS

Studies were conducted on excised shoots of Eastern White Cedar (*Thuja occidentalis* L.). Samples were collected and examined at a field station on Snake Island which is located 1 km off the south shore of Lake Simcoe about 80 km north of Toronto.

Shoots were manipulated to induce xylem water tensions. Three types of experiments were conducted.

(a) **Air Dehydration of Large Shoots.** An apical shoot, 1.0 to 1.5 m long, was harvested, covered with an opaque plastic bag, and the basal end was recut in water. The shoot was allowed to rehydrate overnight in the laboratory. The following morning the shoot was removed from the water, clamped upright, and dehydrated under fluorescent lights augmented by incandescent lamps. The light intensity was nonuniform and low (2–20 μmol m^{-2} s^{-1}). During dehydration subsamples 3 to 6 cm long were periodically removed and the xylem water tension was measured in a Scholander-Hammel pressure bomb. Stomatal conductances were meas-

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[2] Abbreviations: Ψ_{xp}, xylem pressure potential; AE, acoustic emission(s); Ψ_{txp}, threshold xylem pressure potential at which AE begin; dB, decibel.

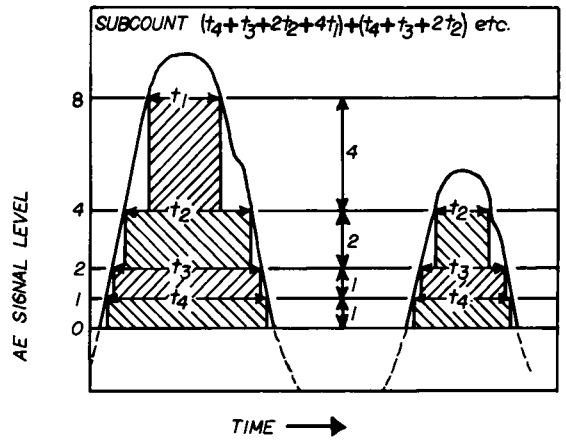

FIG. 1. A diagram showing two positive spikes of an AE and showing how the area under the spike is approximated by rectangular elements. Time, t, is measured by each discriminator clock. Register 4 records time for discriminator 4 which has a discrimination level of 0.25 v; it records subcounts representing t_4 in μs. Register 3 records time for discriminator 3 which has a discrimination level of 0.5 v; it records subcounts representing t_3 in μs. Register 2 is set at 1 v and records subcounts in integer amounts which are multiples of 0.5 μs, so subcounts in this register are equal to $2 \times t_2$. Register 1 is set at 2 v and records subcounts in integer amounts which are multiples of 0.25 μs, so the subcount in this register is equal to $4 \times t_1$. One subcount is thus equal to 2.5×10^{-7} vs in each register.

ured using a null balance porometer (built for Dingbat Electronics by Dr. Ewan Neilson, Aberdeen, Scotland). Evaporative surface areas were estimated by measuring the projected area of green shoots using a LiCor model LI-3000 leaf area meter and applying a conversion factor between projected area and actual area (14).

The AE transducer was clamped firmly against the stem about 30 to 50 cm from the base; to facilitate contact with the sapwood the bark was removed along a 4 to 6 cm length of stem for about one-quarter of the circumference where the AE transducer was clamped. The sapwood was covered with a thin layer of grease to reduce surface drying.

(b) **Air Dehydration of Sapwood Samples.** A shoot 0.5 to 1.5 m long was harvested and stripped of bark, foliage, and branches less than 2 or 3 mm in diameter. The transducer was clamped firmly against the stem and AE were measured while the sample dried in air.

(c) **Pressure Bomb Dehydration of Small Shoots.** An apical shoot was placed in a large pressure bomb and dehydrated to a balance pressure of 2.0 to 2.1 MPa over 2 to 4 h. The shoots were 0.3 to 0.5 m long and the sapwood diameters were 6.5 to 7.5 mm at the base. The AE transducer was placed on the flat cross sectional surface of the stem protruding from the pressure bomb. A concave depression had been milled in the butt end of the stem to accommodate the 'contact sole' of the transducer (see below). Xylem water tensions were developed in the shoot by lowering the bomb pressure below the balance pressure and AE were measured.

We are not aware of any other instance in which ultrasonic AE equipment has been used in the plant sciences; so it is necessary to describe this equipment in some detail. We used a type 8312 AE transducer, a type 2638 wideband conditioning amplifier, and a type 4429 AE pulse analyzer; all supplied by Brüel and Kjaer, Naerum, Denmark.

The transducer uses a piezoelectric crystal element to transduce vibrations to voltage. The frequency response (= voltage output per unit vibrational intensity) is flat to ±10 dB in the frequency range of 100 kHz to 1 MHz. (A decibel is one-twentieth of a logarithmic unit; so 20 dB is a factor of 10 and 10 dB is a factor of about 3.16.) The transducer has a built in low noise preamplifier which boosts the electrical signal from the piezoelectric element by a factor of 40 dB (100 times). The transducer is built in a cylindrical stainless steel package 41 mm in diameter and 25 mm high. Contact between the wood and the sensitive area on the transducer was facilitated by a raised metallic contact sole in the center of the lower surface; the contact sole is about 3 mm in diameter and projects about 0.3 mm below the sensitive surface.

The output of the transducer was connected to the input of the amplifier through a built-in passive filter that passed AC signals in the frequency range of 0.1 to 2 MHz. A combined gain of 81 dB was used in these experiments since this kept the electronic noise originating in the transducer below the minimum discriminator level of the pulse analyzer.

The pulse analyzer was used to estimate the cumulative intensity of AE. It measures the approximate area under positive spikes of the curve of voltage *versus* time of the amplified AE. The analyzer contains 4 voltage discriminators set at 0.25, 0.5, 1, and 2 v. When the input signal exceeds the preset voltage trigger levels of the discriminators, a clock is started which measures the total time during which the signal exceeds the preset voltage level. The time during which the signal level exceeds the four preset trigger levels is measured and, in effect, multiplied (weighted) by the amplitude difference between each level. This results in a measured value approximately proportional to the area under the level *versus* time curve of the AE signal. This relationship is illustrated in the diagram in Figure 1. Each discriminator displays a digital readout (subcount). One subcount corresponds to a rectangular area in Figure 1 of 2.5×10^{-7} vs (volt × second). The four discriminator area values (subcounts) are summed, and the sum (= the approximate area under the curve in Fig. 1) is displayed digitally and also transmitted as an analog signal which can be recorded on a strip chart. The summation register adds the subcounts from the discriminators in multiples of 100, *i.e.* ones and tens digits are dropped. One 'AE count' from this summation register is thus equal to an area of 2.5×10^{-5} vs. We report in this paper AE activity as cumulative counts or as count rates (in cpm) in the summation register. This count does not refer to the total number of AE events (= cavitations?).

The pulse analyzer could not be used as a simple event counter. The relationship between an AE count and the number of events depends on the intensity of the AE emission at its source and the amount by which the vibrations are attenuated while traveling from the source to the AE transducer. It is possible to approximate the number of AE events needed to produce an area of 2.5×10^{-5} vs = 1 count in the summation register. This is done by watching the advance of the readout of the discriminator subcounters which are updated once every 0.1 s. When AE events are occurring at a rate of only a few per minute, then the advance of the subcounter in 0.1-s intervals probably reflects the subcount per event. The mean areas (= counts) for a few hundred AE events were determined in this way.

In some experiments, the summation register did not offer enough resolution in the estimate of the count rate, because the summation counter drops the two least significant figures from the discriminator subcounters. A hundred times increase in measurement resolution was obtained when AE activity was slow by manually reading the numbers from the discriminator subcounters.

To characterize the waveforms of the AE, the AE transducer and amplifier were connected to a wave digitizer. Analog to digital conversions were performed every 0.05 μs and each AE was recorded by 2048 conversions with a resolution of 8 bits (1 part in 256). Analog representations of the AE were transmitted to an X-Y plotter.

RESULTS

AE Waveforms. Several hundred AE waveforms were captured by an analog to digital waveform analyzer and displayed on an

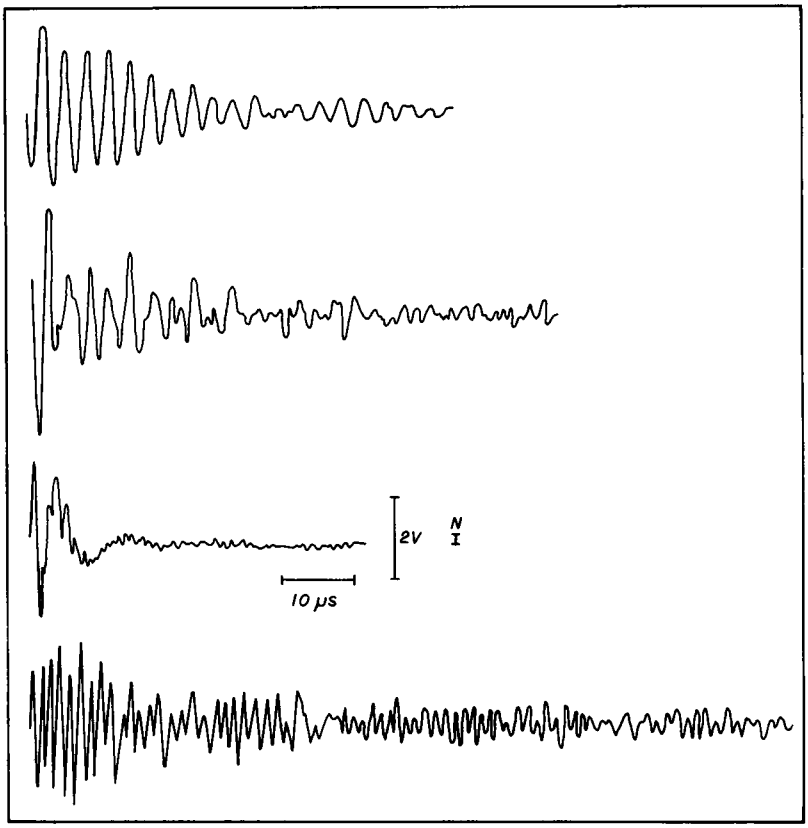

FIG. 2. Four typical AE events. Time scales and voltage scales are indicated by bars. The small bar labeled N represents the peak to peak noise level of the measuring system.

oscilloscope screen. About 20 of these were recorded and four typical waveforms are shown in Figure 2. Each AE had one to three predominant vibrational frequencies, but the vibrational frequencies differed from AE to AE, *e.g.* the upper trace in Figure 2 is mostly 0.35 MHz, the second trace is 0.35 MHz mixed with 0.7 MHz, the third trace is 1 MHz mixed with about 0.1 MHz, and the last trace is 1 MHz with some 0.7 MHz frequencies. With the apparatus used and a gain setting of 81 dB, the typical noise level was less than 0.2 v peak to peak in an oscilloscope sweep lasting 100 μs. The vertical bar marked N in Figure 2 represents 0.25 v peak to peak; any peak to peak oscillation larger than this amplitude is probably caused by an AE vibration.

Relating AE Summation Counts to AE Events. When AE events were occurring at a slow rate, *i.e.* 20 to 80 events/min, we could manually relate the numbers appearing on the discriminator counters to the number of AE events. In one pressure bomb experiment, we recorded 18.8 ± 1.5 AE events/count on the summation counter. The mean was based on 320 events and the quoted error is the SE. In an experiment during which a whole shoot was dehydrated in air, we recorded 5.5 ± 1.1 events/count on the summation counter; the mean and SE being based on 352 events.

AE from Shoots during Air Dehydration. Three apical shoots were air dried over a period of 36 to 72 h. Several factors of all three experiments were reproducible; one result is shown in Figure 3. Typically, the Ψ_{xp} fell from 0 to −2.05 MPa in 4 to 5 h. At a Ψ_{xp} of −1 MPa, AE began. The rate of AE peaked when Ψ_{xp} reached −2 MPa. Over an initial 4- to 5-h period, the stomatal conductance peaked and then fell to low values. The maximum stomatal conductance observed was 0.06 cm s^{-1}, about 0.3 times the maximum value obtained on sunny summer days in field measurements (14). The conductances probably remained low because of the low light levels. In all replicates, Ψ_{xp} fell to a minimum of −2 MPa then rose to about −1.6 MPa during the first 3 to 5 h. Over the next 20 h, Ψ_{xp} gradually fell from about −1.6 to about −2.2 MPa.

AE from Shoots in a Pressure Bomb. Smaller terminal shoots were placed in a pressure bomb and dehydrated by an overpressure to a balance pressure of 2.0 to 2.1 MPa. The AE transducer was placed on the end of the sapwood protruding outside the bomb. At the balance pressure, the Ψ_{xp} is zero, but as the bomb pressure is reduced, Ψ_{xp} decreases by an amount estimated by the difference between the current bomb pressure and the balance pressure. AE were measured from six shoots dehydrated in a pressure bomb. In three cases, the bomb pressure was released rather quickly (in 1 to 5 min) and AE started when the computed Ψ_{xp} reached about −1 MPa. In three other cases, the bomb pressure was reduced in a stepwise fashion over a period of 5 to 8 h. A typical result (Fig. 4) shows that AE became significant when the Ψ_{xp} reached −0.9 to −1.0 MPa. After each stepwise decrease in Ψ_{xp}, there was an immediate increase in AE count rate followed by a lower 'basal rate'. As Ψ_{xp} decreased, the basal rate grew larger. After 5.2 h, the bomb pressure was increased until the computed Ψ_{xp} reached −0.8 MPa and the AE count rate fell nearly to zero.

Control experiments were done in which the shoots were replaced with short wet or dry stem segments mounted in the pressure seal of the pressure bomb. Very little AE activity could be detected from the stem segments as the bomb pressure was raised or lowered over the pressure range of 0 to 2.1 MPa. Thus, the AE activity in Figure 4 was not produced by mechanical stresses and strains in the walls or rubber pressure seal of the pressure bomb.

AE from Sapwood Samples during Air Dehydration. Six shoots from 0.5 to 1.5 m long with basal stem diameters of 6 to 18 mm were harvested and stripped of green shoots and bark; only

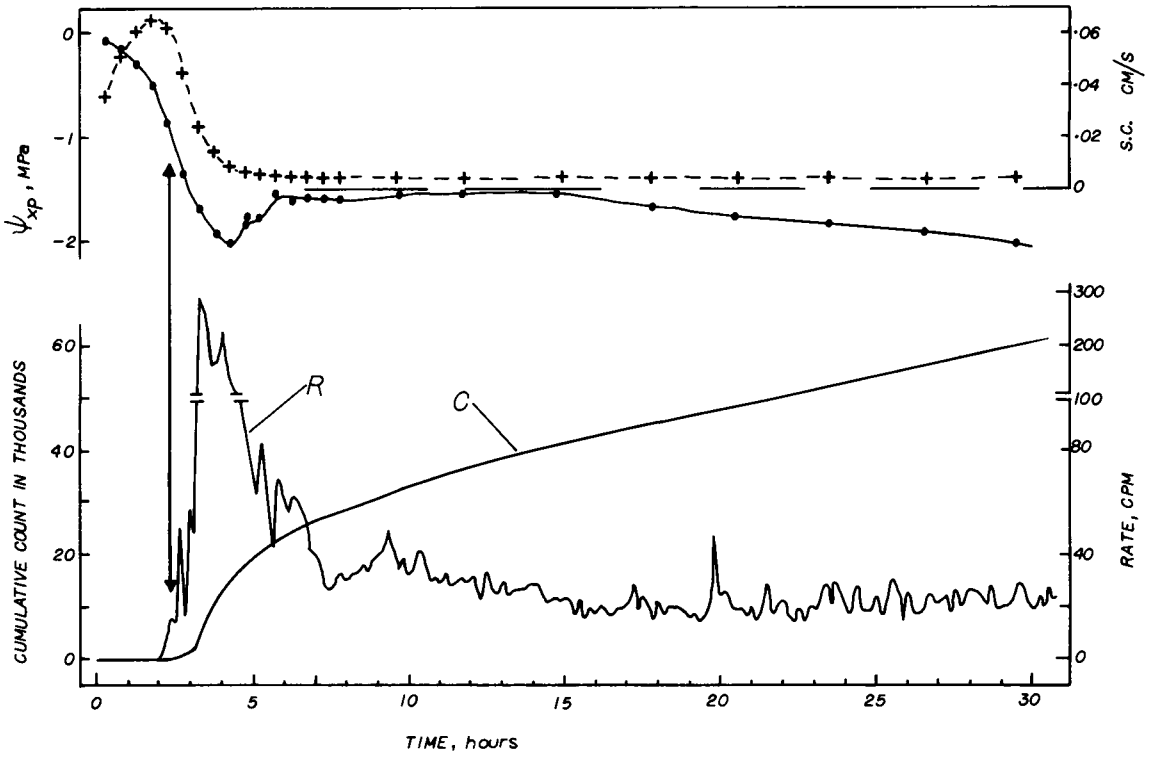

FIG. 3. Time course of the air dehydration of a white cedar shoot. Abscissa = time in hours; lower left ordinate = cumulative AE counts from the summation register (curve C); upper left ordinate = xylem pressure potential in MPa (●——●); lower right ordinate = AE count rate in counts/min from the summation register (cpm, curve R); upper right ordinate = stomatal conductance in cm/s (S. C., + - - - +).

sapwood remained. The AE transducer was clamped to the cylindrical surface of these samples and they were allowed to dehydrate in the air. We did not have equipment to measure Ψ_{xp} in these samples.

In Figure 5A, AE count rates are shown for a large sapwood sample during the first 11 h of air dehydration. At 1.2 and 6.8 h, the basal end of the branch was immersed in water and AE activity rapidly fell to zero. Soon after the water was removed at 2.0 h and 7.6 h, AE activity resumed. At 4 h, lighting was supplemented by two incandescent spot lights which warmed the sapwood. This caused an increase in the evaporation rate from the sapwood, and it also caused an increase in AE count rate which decreased when the supplementary lights were turned off. Acoustic emissions usually ceased after 12 to 30 h depending on the sample size (*e.g.* Fig. 5B).

Qualitatively similar results were obtained when whole shoots were treated by adding and removing water and lights.

DISCUSSION

We have demonstrated that AE in the frequency range of 0.1 to 1 MHz are detectable in *T. occidentalis* (Fig. 1). AE are transmitted as vibrations; we propose four sources of vibrations.

(a) **Oscillation of Hydrogen Bonds in Water.** The hydrogen bonds between water molecules may be viewed as tiny springs. As the water tension develops, the springs will stretch slightly. A cavitation will instantaneously reduce the tension to about −0.1 MPa causing the springs to snap back and perhaps to oscillate a few times before coming to rest.

(b) **Elastic Oscillations in Tracheid Walls.** There is evidence from electron microscopy that xylem vessel walls bend inward when Ψ_{xp} is negative (6), and this is not surprising on physical grounds. Inasmuch as conduit walls exhibit limited elasticity, it is reasonable to assume that they will snap back and oscillate a few times when Ψ_{xp} is instantaneously raised by a cavitation event.

(c) **Torus Aspiration.** When a cavitation occurs, the tori will aspirate, *i.e.* they will be pulled rapidly by the receding water interface towards the pits in the adjacent uncavitated tracheids. The collision of the tori against the pit walls might cause detectable wall vibrations.

(d) **Structural Failure in the Sapwood.** AE occur when most materials are strained, *i.e.* when a deformation takes place. Short impulsive stress waves that are generated at a failure point propagate through the structure; the ultrasonic equipment we are using has been used mostly in the engineering sciences to detect the onset of structural failure at the microscopic level (18).

The evidence we have that AE events are correlated with cavitation events is circumstantial, but our evidence is about as comprehensive as that obtained by Milburn and others in the audio frequency range. Intuitively, we think the following relationships ought to pertain to cavitation events. (a) There ought to be a threshold xylem pressure potential (= Ψ_{txp}) for cavitations. When Ψ_{xp} is higher than the threshold (Ψ_{txp}), there ought to be no cavitations. In *Ricinus*, audio frequency AE start only when Ψ_{xp} falls below −0.5 MPa (9); in *Malus* leaves, the threshold is −1.2 MPa (16). Our results show that the threshold for ultrasonic AE is at −0.9 to −1 MPa in *Thuja* sapwood (Figs. 3 and 4). (b) The rate of cavitations ought to be a function of the amount by which Ψ_{xp} is below the threshold, *i.e.* the rate of cavitations might be some function of $\Psi_{txp} - \Psi_{xp}$, and cavitations should also be a function of the rate of net water loss. In *Ricinus*, the rate of audio frequency AE does increase when conditions are manipulated to increase evaporation rates or $\Psi_{txp} - \Psi_{xp}$ (7, 8, 10). In our experiments, the rate of AE peaked when $\Psi_{txp} - \Psi_{xp}$ was growing fastest and before the stomatal conductance had fallen to the lowest values; see Figure 2 for times from 2 to 4.5 h. Conversely, when water was restored to excised whole shoots (unpublished results) of *T. occidentalis* or to excised sapwood samples (Fig. 5A), AE stopped. When water was removed or the tissue was warmed by supplemental lights, the rate of AE increased (Fig. 5A and unpub-

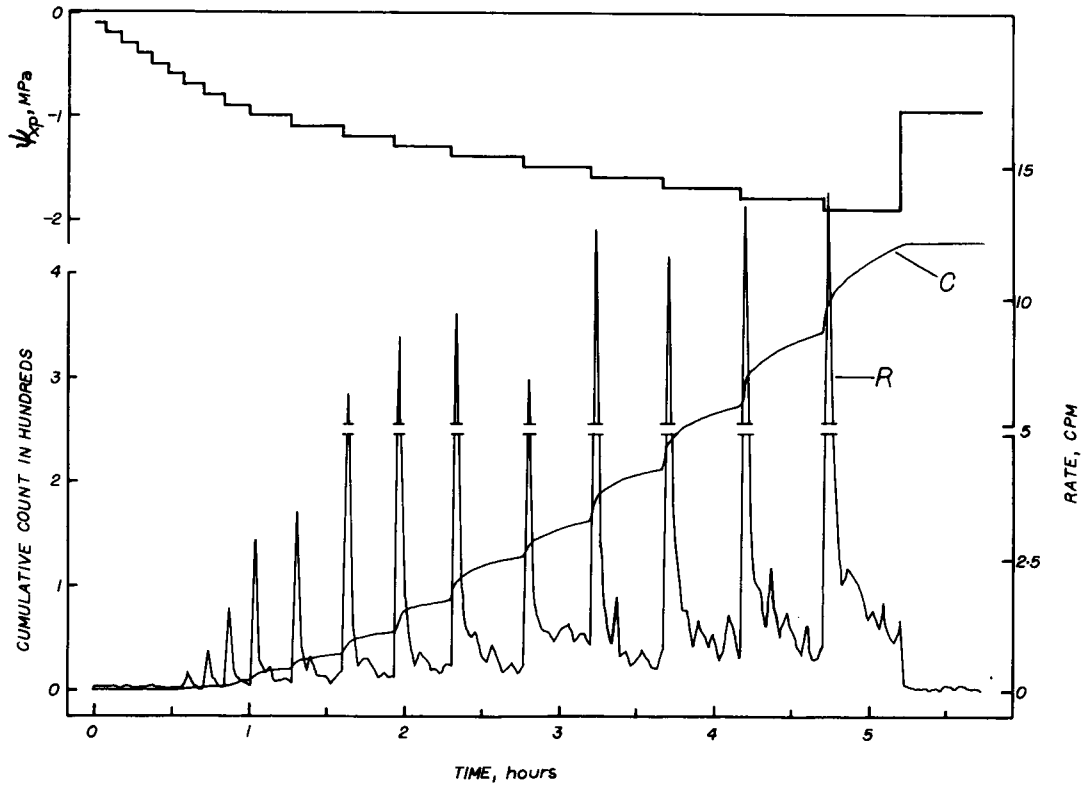

FIG. 4. AE from a shoot in a pressure bomb. The shoot was dehydrated to a balance pressure of 2.0 MPa. The bomb pressure was reduced in a stepwise fashion. The computed xylem pressure potential, Ψ_{xp} = the current bomb pressure minus the balance pressure at the beginning. (The actual Ψ_{xp} is probably less negative than shown here because water from cavitated tracheids would rehydrate surrounding tissue and lower the balance pressure an unknown amount.) Time is on the abscissa and the lower two curves are the cumulative AE count (curve C) and the AE count rate (curve R).

lished results on whole shoots). (c) Cavitations ought to occur rapidly in isolated xylem tissue during air drying because xylem does not shrink much upon drying (xylem is not very elastic) so water loss must proceed with cavitation events. Milburn and McLaughlin (11) have reported audio frequency range AE in isolated vascular bundles of *Plantago major*. L.; during air drying, AE were produced as vascular bundles lost water in a manner similar to that of *Ricinus* but the process was more rapid. We obtained similar results when sapwood samples were air dried (Fig. 5B).

Perhaps the most tantalizing piece of indirect evidence we have that cavitations are occurring at the same time as AE is the evidence of minor green shoot rehydration during continual air drying. In three of three cases, the minor shoots fell to a water potential of −2.0 to −2.1 MPa and then rehydrated to a water potential of −1.55 to −1.65 MPa (see Fig. 3). Similar changes in Ψ_{xp} have been observed in excised conifer shoots (13) but were not correlated with AE. One possible explanation of this is that minor shoots were rehydrated by water released by cavitated tracheids. Using water potential isotherm curves (14) and measurements of the total leaf and stem mass in the shoot in Figure 3, we have estimated the total amount of water needed to increase the shoot water potential from −2.0 to −1.6 MPa. If all the water came from the wood, then the water content of the wood would have fallen 8.6% from its value at full hydration. However, we have not yet confirmed this by independent measurements of the sapwood water content in the course of the dehydration experiments. Some of the water contributing to the rehydration of the minor green shoots could have come from the bark so the amount of water coming from the sapwood could have been less than 8.6% of its value at full hydration. We have rejected the possibility that the water could have come from less dehydrated minor green shoots because pressure bomb subsamples were always taken from the regions of the excised shoot under lowest light intensity; the more brightly illuminated shoots ought to have been at the lowest water potential at the time of stomatal closure.

It is of interest to compare the number of AE events to the number of tracheids in the sapwood of *T. occidentalis*. In cross section, the tracheids are square to slightly rectangular. Taking their typical dimensions to be about 20 × 20 μm and 2.5 mm long, there are about 1×10^6 tracheids/cm^3 of sapwood; dimensions were taken from References 1, 2, and 5. Over a period of 30 h, the summation counter incremented to a count of about 60,000 in Figure 3; we think that each count represents about 5.5 AE events in this type of experiment. So we think a count of 60,000 represents about 3.3×10^5 cavitations. Preliminary results (unpublished) indicate that we can detect AE within several cm of the detector; so we are measuring AE from several cm^3 of tissue; thus, the estimated number of events is reasonable.

The estimated number of AE events per count in pressure bomb experiments (18.8 events/count) is more than measured from larger shoots dehydrated outside the pressure bomb. But in the experiments in which shoots were air dehydrated the transducer was mounted on the cylindrical surface of the sapwood, whereas in the pressure bomb the transducer was on the butt end of the shoot; therefore, in the first case vibrations were measured in the radial direction and in the second case vibrations were measured in the longitudinal direction. Given that the elastic properties of wood are different in the two directions, it is probably reasonable to predict that vibrations would be propagated more vigorously in the radial direction than in the longitudinal direction. We observed larger amplitude signals when AE were measured with the transducer on the cylindrical surface than with the transducer on the butt end of shoots. This could explain the difference in AE events

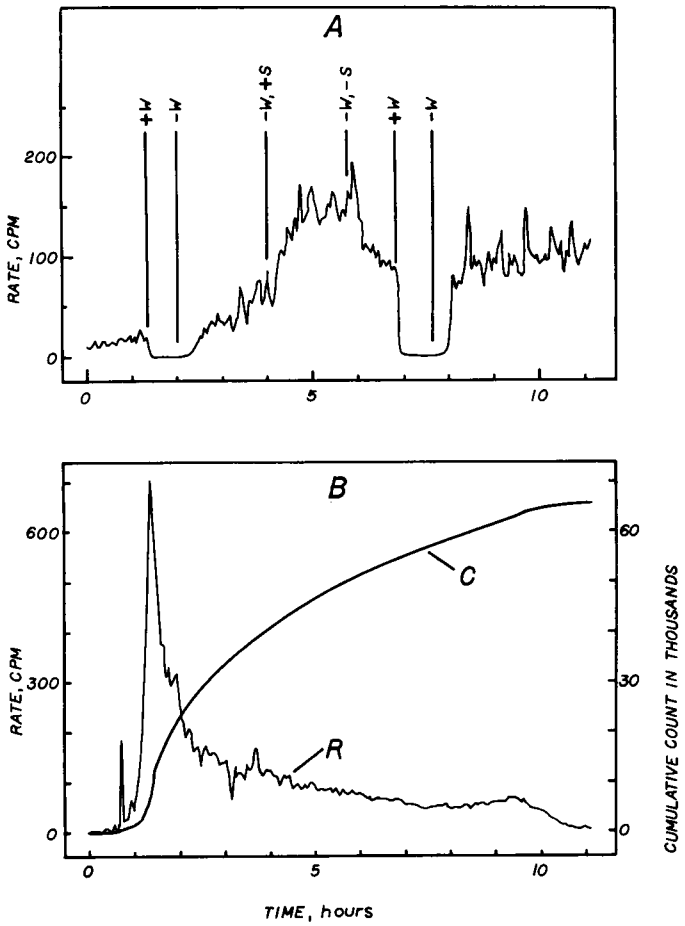

FIG. 5. AE from sapwood samples during air dehydration. Time is on the abscissa. A, AE count rates *versus* time under various conditions: +w = base of sapwood sample immersed in water, −w = water removed, +s = supplementary incandescent light on and sapwood temperature and evaporation rate rises, −s = supplementary lights off. B, AE cumulative counts (curve C) and AE count rates (curve R) for a sapwood sample during air dehydration. After 11 h, all AE activity stopped.

per AE count in the two experiments. It is also possible that some of the vibrational energy was dissipated in the rubber pressure seal when the shoots were mounted in the bomb; this would reduce the average intensity of each signal contributing to a count.

The ultrasonic equipment we have used is much better than the audio frequency range equipment used to date because ultrasonic AE can be measured free of audio frequency noise. The plants can now be manipulated and standard laboratory procedures can now be undertaken simultaneously with AE measurements. If it can be proved that most ultrasonic AE are a result of cavitation events, then we will have a powerful diagnostic tool that may give us new insight into the water relations of trees and other plants.

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