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*Communication*

# Detection of Xylem Cavitation in Corn under Field Conditions[1]

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## ABSTRACT

**We report the detection of cavitation events in corn (*Zea mays*) plants growing under field conditions in Greeley, CO. To our knowledge this study reports the first successful attempt to monitor continuously for long periods the cavitation events of a crop plant using acoustic detection techniques. Cavitation events occur in corn plants using acoustic detection techniques. Cavitation events occur in corn plants irrigated daily when the xylem pressure potentials fall below about −1.0 megapascals. In unirrigated corn we estimate that approximately half of all vessels cavitate on any one day when xylem pressure potentials fall below about −1.8 megapascals. We postulate that root pressure developed every night in irrigated and unirrigated corn is adequate to rejoin cavitated water columns.**

Ever since the introduction of the cohesion theory of sap ascent in plants (1), it has been recognized that water in the conduits (vessels and tracheids) of xylem can be under considerable negative pressure. Typically, xylem functions at pressure potentials between −1.0 and −3.0 MPa, with atmospheric being zero, and vacuum about −0.1 MPa. Because the vapor pressure of water is slightly above vacuum, liquid water in the xylem at pressures below this is in a metastable state. Thus xylem has been aptly termed the "vulnerable pipeline." At the moment the metastable state is disrupted, the xylem water undergoes an explosive phase change, called a cavitation event, and the xylem conduit is left with a near vacuum filled only with wator vapor. The cavitated conduit soon becomes embolized, *i.e.* fills with air that comes out of solution from surrounding water.

According to the cohesion theory of sap ascent, the intermolecular bonds between water molecules or between water and solids in xylem conduits are sufficient to maintain the continuity of water columns in xylem. The cohesion theory has become so widely accepted among plant biologists that the feeling has arisen that, if cavitation events occur at all, they must be very rare events under normal growth conditions (*e.g.* Ref. 11). Contrary evidence has begun to emerge. For some time it has been suspected that cavitation events are accompanied by detectable acoustic emissions (AEs[5]) in the audible frequency range (6–9). It has also been shown that these AEs can be detected in some small herbs (*Plantago*); audible AEs occur at xylem pressure potentials normally encountered under field conditions, *i.e.* −0.5 to −1.5 MPa (10).

Unfortunately, Milburn's method (6–10) of detecting cavitation events thorugh the amplification of audible AEs has serious limitations. The two most important limitations being that AE counting must be done manually through aural detection and that the audible AEs from cavitation events are easily masked by ambient sound emissions from other sources. Recently, it has been shown that plants under drought stress produce ultrasonic AEs in the frequency range of 0.1 to 2.0 MHz. It has been clearly established that these ultrasonic AEs are reliable indicators of cavitation events (2, 13–16). Furthermore, ultrasonic AEs are not masked by ambient noise and can be easily counted by suitable electronic circuits. Given the water potentials at which cavitation events occur in various species (12, 14) it would appear that cavitation events are common daily occurrences in some species (*e.g. Thuja* and *Rhapis*) and comparatively rare in others (*e.g. Tsuga* and *Acer*).

Little is known about the relative vulnerability to cavitation of the xylem conduits of common crop plants and no long-term measurements of cavitation events under field conditions have been undertaken. If it can be established that cavitation events do occur in some or all crop plants, it would clearly point to the necessity of learning more about the mechanisms of cavitation resistance and avoidance and mechanisms of embolism dissolution. In this paper we show that cavitation events are common occurrences in corn (*Zea mays*) grown under field conditions. This suggests that much more work needs to be done on cavitation events in crop plants if we are to fully understand all aspects of drought physiology.

## MATERIALS AND METHODS

Corn (*Zea mays* cv Garst 3732) plants were grown at the Northern Colorado Research Demonstration Center near Greeley, CO. The growth plot was divided into well watered control and droughted plots. The control plots were watered daily. The droughted plots were not watered until a desired water stress level was achieved. All plots were under continuous computer control as described by Fiscus *et al.* (3). Briefly the computer monitored at 10 min intervals the following parameters: air temperature, solar radiation, RH, and the pressure drop in several mass flow porometers. At midnight of each day the computer calculated the relative stomatal opening (4) and an ISO. The latter was expressed as a fraction of the maximum possible value

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[5] Abbreviations: AE, acoustic emission; ISO, integrated stomatal opening; FISO, fractional integrated stomatal opening.

of ISO for well watered controls under that day's light conditions (FISO). The computer was programmed to use this information to decide when a trickle irrigation system needed to be turned on to maintain a preset water stress as measured by FISO. Several weeks of drought are required to reach low values of FISO. Most of our measurements were conducted in the time period during which FISO was decreasing, *i.e.* while drought stress was increasing.

Ultrasonic AEs were measured using a Bruel and Kjaer model 8312 broad band transducer. The AEs were amplified by a factor of 74 dB and passed through a high pass filter with a frequency cut off of 100 kHz. The AEs were counted by the computer assisted methods described elsewhere (15, 16). Ultrasonic AEs have been shown to correlate well with xylem cavitation events in woody plants (14).

Three portable AE counters were constructed for field based measurements at the Greeley site. The AE counter had a custom made AE signal amplifier. The digital part of the counter was based upon a single board computer (Z80 Starter Kit, SD Systems, P.O. Box 28810, Dallas, TX) to which was added 9 K of additional RAM, 2 K of extra ROM, an Intel 8253 clock/timer circuit for AE counting, an LM360 high speed comparator, and a digital to analog converter. A control program was written in Z80 assembly language and placed on a 2 K EPROM which programmed the unit to do the following: (a) display cumulative AE events on a six digit LED display with an update once per second, (b) output to an analog strip chart recorder a voltage proportional to the rate of AE events updated once per second, (c) save in RAM the number of AE events that have occurred in each 30 s interval, (d) save the data stored in RAM on demand on a cassette tape recorder, and (e) replot data (from RAM or cassette tape) on a strip chart recorder as cumulative events or rates of AEs *versus* time on a strip chart recorder. Schematics and ROM program source listings for our instrument are available from M. T. Tyree. Details are not presented here since a much more advanced instrument of equal cost has since been developed by M. T. Tyree and will be described elsewhere.

The AE transducer was attached to the second internode above ground level. In most plants the leaf sheath covering the internode had already fallen off. If the sheath was still present it was removed to facilitate attachment of the AE transducer. Only two AE counters were used in the field at any one time (the third was kept for laboratory based experiments and as a backup in case of equipment failure in the field). One transducer of one AE counter was attached to a corn internode. The other AE counter was placed in the same part of the field but the transducer was not attached to a corn plant. The second AE counter served as a 'background' counter to provide some measure of background counts caused by internal electrical noise in the amplifiers and caused by the electrical interference of thunder storms and power line surges. Thus AEs from droughted and control plants were measured on separate but comparable days.

On selected days throughout the drought cycle measurements of leaf water potential and stomatal conductance were made at hourly intervals. Leaf water potentials were measured on excised corn leaves in a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA). Stomatal conductances were measured with a Li-Cor model 1600 porometer.

## RESULTS AND DISCUSSION

The soil of all plots were originally at field capacity when corn seed were sown. Several weeks were required before soil water potentials fell low enough in the advancing roof profile for substantial water stress to develop. By Julian day 216 (August 4, 1984) the cumulative AE events per day had risen above 1000 AEs/d; typical background counts were <300 Aes/d. Cumulative AE events per day is plotted *versus* Julian day in Figure 1.

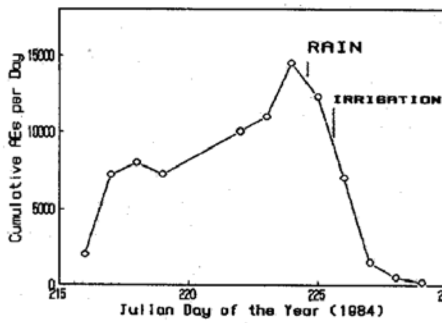


FIG. 1. Cumulative acoustic emissions (=cavitation events) recorded each 24 h period in field grown, unirrigated corn *versus* Julian day.

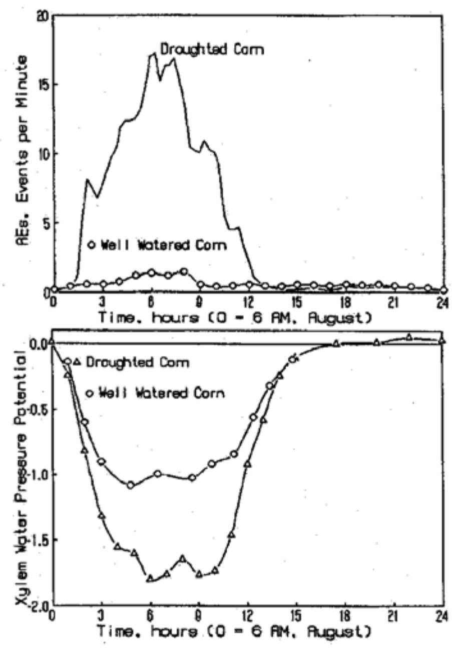


FIG. 2. The upper graph shows the rate of acoustic emissions (=cavitation events) in well watered and droughted corn *versus* time of day in August 1984. The lower graph shows the xylem pressure potential measured with a pressure bomb in the same plants as above *versus* time of day.

Overnight between days 224 and 225 a significant rain fall occurred. On the next day the corn was irrigated. It can be seen that within a few days of rain and irrigation the cumulative AEs per day fell back to the background level. From days 216 to 224 the fractional integrated stomatal opening (FISO) was in the range of 0.3 to 0.2 with no particular trend toward higher or lower values. The midday water potentials of the corn plants were in the range of −1.6 to −2.0 MPa on days 214 to 224. A qualitatively similar pattern of events occurred in the 1985 growth season.

A diurnal time course for Julian day 219 is shown in Figure 2. The upper curve shows the rate of AEs *versus* time in droughted corn. In the lower curve are leaf water potentials measured by the pressure chamber technique. Superimposed on Figure 2 are comparable data from well watered controls measured 12 d later on a comparable sunny, warm, and dry day. None of the curves is corrected for background AE counts. The nighttime levels can be taken as representative background count levels. Note that daytime AE rates are above background levels even in well watered corn plants.

We do not know whether the AEs detected in corn stems reflect cavitation events in xylem vessels or in other structural components, *e.g.* xylem tracheids or sclerenchyma lumina. In other species studied (*Acer saccharum, Tsuga canadensis*, and *Thuja occidentalis*) large xylem elements do cavitate before small ones. So it seems probable to us that AEs do represent cavitation events in vessels of corn. Even in well watered corn cavitation events were detectable at leaf water potentials ranged from −0.9 to −1.1 MPa. The well watered corn plants exhibited the distinct leaf curl characteristic of water stress in the species on warm, sunny and dry days. Cavitation events occur in significant numbers in droughted corn. The longest corn vessels are up to 10 or 15 cm long with a median length of about 2 cm (results based on plant perfusion experiments (17) attempted at Ft. Collins). Using our best estimates of the maximum listening distance of the AE transducer, of the number of vessels in a corn stem cross-section, and of vessel lengths, we have estimated that there are perhaps 30,000 to 40,000 vessels within the listening distance of the transducer. Thus approximately half of the vessels cavitate on any given day in our droughted corn plants.

Our observation of significant numbers of cavitation events within a diurnal cycle is not new. Similar observations have been made in small herbaceous plants such as *Plantago* and *Tussilago* (10). In *Plantago* all vessels cavitate when the leaf water potential ranges from −0.5 to −1.5 MPa. Milburn and McLaughlin (10) have suggested that cavitated vessels of these species refill by root pressure observed in *Plantago* and *Tussilago* every night; in these species guttation is a common observation. In corn plants root pressure could also refill cavitated vessels. Even in the droughted plants the leaf water potential was so near zero at dawn that it could not be measured in excised leaves in the pressure chamber. Indeed excised leaves frequently appeared to bleed xylem sap immediately after excision. Droughted corn plants and well watered controls both bleed sap from the root systems after excision at ground level. For technical reasons we could not measure the magnitude of the positive pressure in the xylem of corn plants at dawn, but we have plotted positive values of about 0.04 MPa in Figure 2 to indicate what we think might be reasonable values to expect. The vascular bundles of corn always have tracheids next to vessels (5). Since tracheids are less likely to cavitate than vessels we suggest that tracheids are there to maintain a residual amount of xylem conduction during periods of drought stress. Tracheids may also facilitate refilling of vessels by root pressure.

Although we cannot say that AEs detected in corn represent cavitation events in xylem vessels, the AEs are very likely to indicate cavitation events in some cellular luminae and will thus indicate the onset of drought stress and loss of crop yield. In previous years a sustained drop in FISO similar to the levels reported above were enough to reduce yields by about 30% (3). The detection of AE events may be a useful early warning measure of significant drought stress in corn plants. In future work we hope to investigate the possibility of using the AE detectors as irrigation management tools.

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