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Acoustic emission analysis and experiments with physical model systems reveal a peculiar nature of the xylem tension

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Summary

Advanced acoustic emission analysis, special microscopic examinations and experiments with physical model systems give reasons for the assumption that the tension in the water conducting system of vascular plants is caused by countless minute gas bubbles strongly adhering to the hydrophobic lignin domains of the xylem vessel walls. We ascertained these bubbles for several species of temperate deciduous trees and conifers. It is our hypothesis that the coherent bubble system of the xylem conduits operates as a force-transmitting medium that is capable of transporting water in traveling peristaltic waves. By virtue of the high elasticity of the gas bubbles, the hydro-pneumatic bubble system is capable of cyclic storing and releasing of energy. We consider the abrupt regrouping of the wall adherent bubble system to be the origin of acoustic emissions from plants. For *Ulmus glabra*, we recorded violent acoustic activity during both transpiration and re-hydration. The frequency spectrum and the waveforms of the detected acoustic emissions contradict traditional assumptions according to which acoustic emissions are caused by cavitation disruption of the stressed water column. We consider negative pressure in terms of the cohesion theory to be mimicked by the tension of the wall adherent bubble system.

Abbreviations: A, surface area; AE, acoustic emissions; AAE, audible acoustic emissions; CLSM, confocal laser scanning microscopy; *E*, total energy; *F*, gravitational force; *n*, moles; *p*, pressure; *s*, translation; *S*, entropy; *V*, volume; *T*, temperature; UAE, ultrasonic acoustic emissions; ε modulus of elasticity; μ, chemical potential; σ, surface tension; τ, three-dimensional distortion.

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Introduction

The predominantly passive character of long-distance water transport has frequently been questioned. However, it has been repeatedly demonstrated, even in context of acoustic emissions (Borghetti et al., 1991), that the application of poisons as metabolic inhibitors to the water transport system has little or no effect on water movement, reinforcing the concept that non-living cells are primarily involved in water transport and no essential input of metabolic energy takes place. Despite this, various suggestions of active pumping have been proposed time and again, but no mechanical or biochemical devices that could achieve such pumping have been found. Also, the frequently cited root pressure would not be capable of transporting water to the tops of tall trees. In sum, the idea of the cohesion theory that water ascends in the apoplast part of the xylem, largely under the direct influence of the evaporation from the leaves, is most likely the correct explanation, but the transmission of pulling forces through the water column is still puzzling.

Milburn and Johnson (1966) reported that transpiring plants generate acoustic emissions in the audio frequency range. Since that time, Milburn's findings have been considered proof of the validity of the cohesion theory, according to which the ascent of sap is caused by a gradient of negative pressure. The cohesion theory has been repeatedly questioned from a physical point of view because the claimed metastability of water under negative pressure has not been demonstrated for air saturated water. However, the soil water taken up by the roots is air saturated. Despite this inconsistency, challengers of the cohesion theory are usually rejected with reference to the acoustic emissions discovered by Milburn. Seen in the light of the cohesion theory, the acoustic emissions are caused by cavitation-disruptions of the water column under negative pressure. This argument was weakened when Tyree and Dixon (1983) introduced the ultrasonic frequency range into the investigations. It has now become clear that the AAE is only the tip of the iceberg. The overabundance of the UAE turned out to be a problem. Presupposing that each acoustic event is attributable to a cavitation event, it appears impossible to place the countless cavitation defects within the limited number of water conducting conduits. The problem is compounded since the cavitation-defects are supposed to be instantly embolized by air, and therefore the affected vessel tubes malfunction. Several assumptions of incessant embolism repair have been made recently by Zwieniecki and Holbrook (2000). However, a demonstrable repair mechanism has not been found to date.

Simultaneous monitoring of AAE and UAE by Ritman and Milburn (1990) revealed a significant time pattern of the acoustic emissions with leading UAE for intense transpiration and rising AAE for declining transpiration. Unfortunately, these authors eliminated the acoustic emissions during the nightly re-hydration phase. Apparently, the AE-signals of the re-hydration phase could not be explained within the context of cohesion theory. Milburn (1993) suggested that the mysterious UAE be ignored, and considered the AAE to be the most reliable indicator of cavitation. In a previous investigation, we argued that the acoustic emissions from plants are not caused by cavitation under negative pressure, but by sudden surface rearrangements of groups of wall adherent microbubbles under positive pressure (Laschimke, 1989). The existence of gas bubbles in the xylem conduits has been known for years. It is generally known that gas bubbles, which fill the whole lumen of the vessels, form so-called Jamin chains. The Jamin chains do not contribute to the driving forces of water transport; rather, they are barriers. The discovered wall adherent microbubbles, however, are much smaller in diameter than the vessels tubes. Such bubbles are largely stable and do not immediately result in embolism. When we presented the first micrographs in 1989, the microbubbles seemed to be an absurdity, seen in the light of the governing cohesion theory. On the other hand, Zimmermann and co-workers regarded the wall adherent microbubbles as an attractive concept of water transport by Marangoni-forces (Zimmermann et al., 1993). Marangoni flow requires a permanent concentration gradient in the transported water. This gradient has been taken for granted by Zimmermann, but no evidence could be provided up to now. Because Marangoni flow scarcely generates acoustic emissions, Zimmermann took into consideration several other acoustic origins, such as aspirating pits, occurrence of flow turbulence, fusion of gas bubbles adhering to the walls, cracks in the cell walls under strain, drying out of the bark, shrinking of the stem diameter and xylem bending (Zimmermann et al., 2004). Aiming to shed more light on the mysterious acoustic emissions from plants, we applied advanced methods of event detection and AE-analysis. By means of a special arrangement of the acoustic sensors, we were able to eliminate some of the named dubious origins of AE signals. In order to substantiate the results of our acoustic emission testing, we furthered our investigations