Listening to Thirsty Plants

John W. Einset

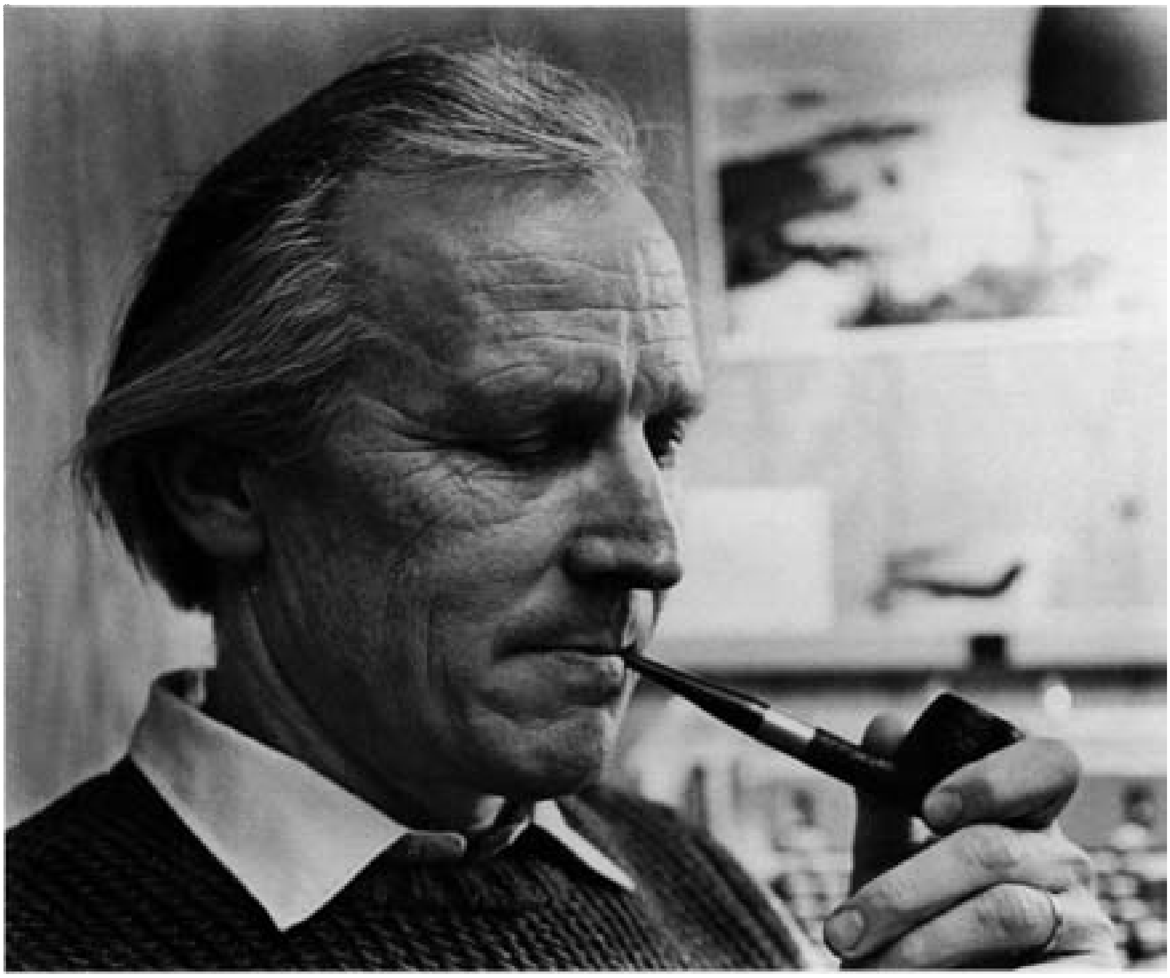
The ingenious application of acoustic devices enables botanists to study the water economy of woody plants

Martin H. Zimmermann, the late Charles Bullard Professor at Harvard University and Director of the Harvard Forest from 1970 to 1984, was a recognized expert on the water economy of plants, especially trees. Among his many contributions to science was the introduction of the term *hydraulic architecture,* a term that describes the way in which plants use their structures to regulate water flow. In fact, a major goal of Professor Zimmermann's research involved detailed descriptions of hydraulic architecture in plants, a task he approached with ingenuity, often using techniques he had developed himself.

As so often happens in scientific research, one of the best ways of understanding a process is to study what happens when it is disrupted. For example, if one is interested in how water moves through a plant, one can ask what happens when water is no longer supplied. The immediate consequence, of course, is that the overall water content of the plant begins to decrease as a result of continued evaporation (*transpiration*) from leaves in the absence of a corresponding uptake of water by its roots. As further drying occurs, the pores (*stomates*) on leaves usually close, thus minimizing additional water loss. Then the stem begins to contract under the tension caused by the evaporation of water from within it. Eventually, dehydration of the stem results in *cavitation* within individual vessels (water-conducting "pipelines") of the xylem as air bubbles replace water. At this stage, flow within the plant ceases because cavitated vessels can no longer transport water. Some plants, in fact, are damaged beyond recovery by cavitation since they are incapable of refilling air-plugged xylem even when water again becomes plentiful.

Sabotage by Bubbles of Air

According to a widely held theory, elaborated in large part by Martin Zimmermann, cavitation is initiated when a tiny bubble of air penetrates a water-containing xylem vessel from an adjacent, dry vessel element—a process known as *air seeding.* Negative hydrostatic pressure within the vessel then causes the bubble to expand quickly and fill the contents of the cell. While the air-seeding hypothesis has not been proven conclusively, it is generally considered to be the best current explanation for cavitation. At the very least, Zimmermann's theory focusses interest on this important phenomenon and stimulates research that could lead to new technology. If cavitation can be better understood, perhaps it can be avoided by breeding plants

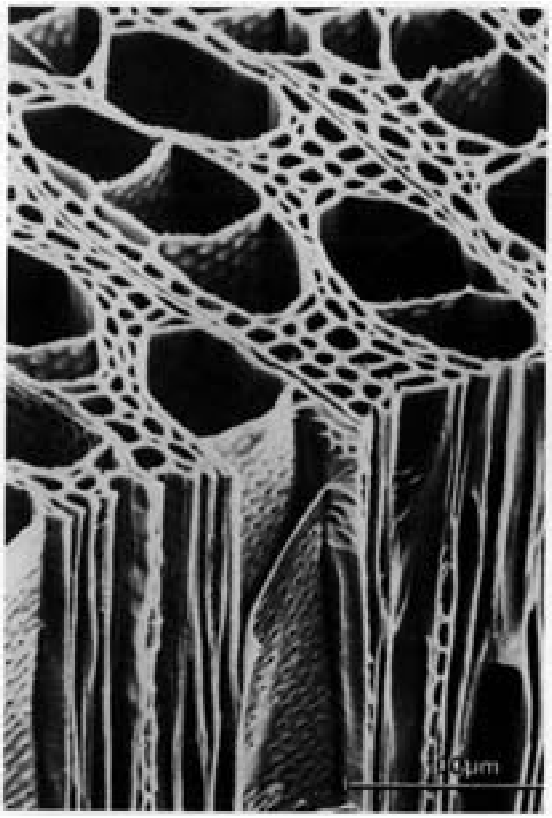


Dr Martin H Zimmermann, the late Director of the Harvard Forest in Petersham, Massachusetts. Photograph by Regula Zimmermann Courtesy of the Harvard Forest

with more effective mechanisms for preventing it. Or, improved procedures might be developed to reverse cavitation once it has occurred.

If the crucial event that sparks cavitation actually is the appearance of an air bubble, the obvious strategy for stopping cavitation is to prevent air from moving between cells. In plants suffering a moderate degree of water stress, this normally is accomplished by the cellulosic cell walls between adjacent elements. An illustration of the principle involved can be obtained by trying to plunge a fresh tea bag directly into hot water. The low permeability of the wet, cellulosic paper causes the tea bag initially to float on the surface of the water until air has diffused out of the bag. The same phenomenon is exploited in life-saving when a shirt or pillow case is used to improvise an emergency flotation device. In these cases, wet fabric impedes the diffusion of the entrapped air.

The relative permeability to air, of a plant cell wall or of any other wet barrier for that matter, can be calculated from physical laws based on the size of the pores it contains: the smaller the pore size, the greater the pressure difference required to push air through it. Given an average pore diameter of about 0.2 micrometer (approximately one ten millionth of an inch) in plant cell walls, the pressure differential necessary for air to move from one cell to another is about 10 to 1. In other words, one can expect air seeding to occur in trees as soon as vessel tensions reach values of minus 10 atmospheres and less.



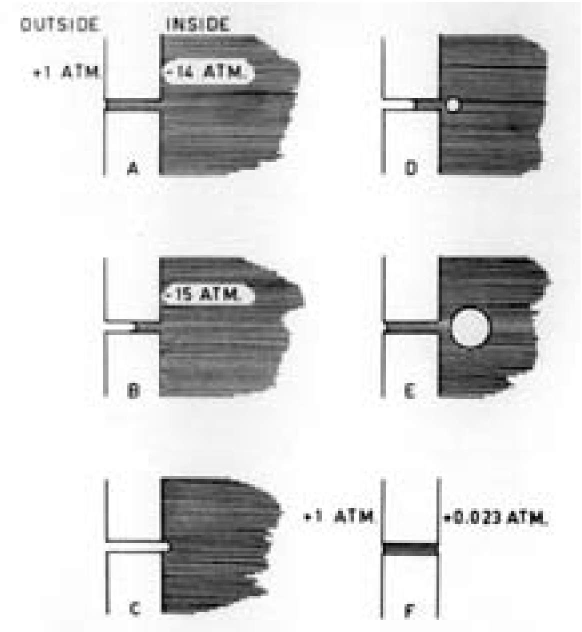
*A scanning electron microscope picture, highly magnified, of poplar (*Populus grandidentata*) wood showing the three-dimensional structure of xylem tissue and individual vessels (the large columnar cells with conspicuous pores on their lateral walls) making up the water-transporting system Courtesy of Springer-Verlag.*

Acoustic Emission: The Sound of Cavitation

Using microscopic techniques coupled with cinematography, Ann M. Lewis (a student at the Harvard Forest) has determined that the lapse of time from the first appearance of an air bubble in a vessel until the end of the cavitation event is less than 1/124 second. The rapidity of this process probably accounts for one of the most important aspects of cavitation—namely, the production of a weak but detectable noise as vessel walls vibrate in response to the air bubble's explosive expansion.

Studies of the "acoustic emissions" (AEs) accompanying cavitations have recently become an especially active area for scientific investigation. At the University of Toronto in Canada, for example, Professor Melvin Tyree has adapted the sensitive acoustic devices used in mechanical engineering to the study of AEs in white cedar (*Thuja occidentalis*) and hemlock (*Tsuga canadensis*) trees. Tyree clamps a noise detector onto the stem of a tree and then monitors AEs as the tree becomes more and more dehydrated. Each signal the detector picks up is processed with the aid of a computer, which analyzes harmonic frequency, duration, and intensity. By doing this, Tyree can exclude interfering signals caused by extraneous (*i.e.*, noncavitation) noises.

This sophisticated instrumentation has already made it possible to prove that individual AEs correspond to single cavitations occurring in the wood of trees; thus, a small (4-mm-diameter, 10-mm-length) block of hemlock wood, for example, contains about one million tracheids (tracheids, rather than vessel elements, are the water-conducting cells of gymnosperms) and produces approximately that number of AEs upon complete dehydration. The technology also makes it possible to measure the potential of different water-transporting systems to recover from cavitation. This can be accomplished by monitoring AEs during the dehydration of a wood sample, then rewetting the sample to its maximum extent and determining the total number of AEs obtained during a second dehydration treatment. Presumably, the difference in AE totals is the number of cells that cavitated beyond recovery during the initial dehydration. Alternatively, AE technolgy can be used to determine the types of cells that are most prone to cavitation, inasmuch as the harmonic frequency of an AE is apparently related to a cell's dimensions. Evidence to date confirms Zimmermann's theory that large vessels, and thus "ring-porous" trees such as oaks and elms, are more likely to cavitate than small vessels, and thus "diffuse-porous" trees such as maples.



M. H. Zimmermann's diagram of the stages involved in cavitation by air seeding. Each panel indicates the status of an air-filled vessel or tracheid (outside) and an adjacent vessel or tracheid (inside) undergoing cavitation. A through C show the effect of progressively negative xylem pressures in causing air movement through a small pore in the cell wall. In D, an air bubble has appeared within the water-containing cell, while E and F indicate the explosive expansion of this bubble that results in cavitation and, significantly, in the acoustic emission. Courtesy of Springer-Verlag.

Practical Applications

Of course, the greatest value of listening to thirsty plants ultimately will be improved understanding of water flow and the mechanisms by which plants prevent damage associated with dehydration. When one considers that water utilization is one of the major factors determining plant growth and survival as well as plant distribution in the environment, it is easy to appreciate how even small advances in scientific knowledge about the water economy of plants can have profound practical consequences.

Martin Zimmermann's book *Xylem Structure and the Ascent of Sap* was dedicated to the memory of Godfrey Lowell Cabot, who in 1937 established the Maria Moors Cabot Foundation for Botanical Research at Harvard University. In the dedication of the book, Professor Zimmermann describes his first meeting with Cabot in the mid-1950s, an occasion that he took advantage of to explain his latest scientific findings in great detail:

> When I had finished, he surprised me with the sudden question, "How can you improve the growth of trees?" This caught me completely unprepared, because I had never thought about practical applications. After what seemed to me a rather painful silence I ventured that it would be useful to learn more about how trees function and grow. He seemed to be quite satisfied with this answer. Little did I guess that trees would be holding me under their spell for so many years!

John W. Einset, associate professor of biology in Harvard University, directs the Arnold Arboretum's Laboratory of Comparative Physiology. In May, he will teach "Tissue-Culture Propagation Methods: An Introduction to a New Branch of Plant Science," a special class limited to Friends of the Arnold Arboretum.