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Trends in Plant Science

Opinion

Talk is cheap: rediscovering sounds made by plants

Andrea Nardini [1,*], Hervé Cochard [2], and Stefan Mayr [3]

A recent study and related commentaries have raised new interest in the phenomenon of ultrasonic sound production by plants exposed to stress, especially drought. While recent technological advancements have allowed the demonstration that these sounds can propagate in the air surrounding plants, we remind readers here that research on sound production by plants is more than 100 years old. The mechanisms and patterns of sound emission from plants subjected to different stress factors are also reasonably understood, thanks to the pioneering work of John Milburn and others. By contrast, experimental evidence for a role of these sounds in plant–animal or plant–plant communication remains lacking and, at present, these ideas remain highly speculative.

Highlights

Recent reports of airborne sound emissions by plants under drought stress have generated interest, leading to speculative ideas on plant–animal and plant–plant communication.

Research on sound production by plants is more than 100 years old, with John Milburn demonstrating in 1966 that these sounds are mainly produced by xylem cavitation events and can be detected with dedicated instruments.

Research from 1970 onward has shown that sounds can also be produced by other passive physical processes in plants, and also demonstrated that acoustic emissions can be used to monitor the water status of plants in the field.

The hypothesis that sounds produced by plants are informative for insects feeding on stressed plants, or even for neighboring plants, is attractive but still purely speculative to date.

Remembering historical milestones

In the recent Spotlight in *Trends in Plant Science* “Plants ‘cry’ for help through acoustic signals” [1], Waqas *et al.* present a study by Khait *et al.* [2] reporting **ultrasonic acoustic emissions (UAEs)** (see Glossary) produced by plants. In the same issue, Hussain *et al.* [3] comment on the same study, and propose several open questions and some speculations on this subject. In the study by Khait *et al.* [2], ultrasonic signals (frequencies of 20–150 kHz) were recorded via microphones positioned at some distance from plants placed in acoustic chambers or greenhouses. By filtering background noise, it was possible to demonstrate that drought-stressed and cut tomato plants (as well as specimens infected with tobacco mosaic virus) emitted more airborne ultrasonic signals compared with control plants. Ultrasonic activities of drought-stressed plants showed a diurnal course with a midday depression, which was related to stomatal regulation. Airborne ultrasonic signals were also detected from other species analyzed except the two woody species (almond and grapevine). The authors suggested that cavitation events in the xylem sap cause UAEs, and also speculated that quantitative and qualitative acoustic information might be used by researchers to identify specific stress situations experienced by plants. They also suggested that airborne sounds produced by plants might be detected by insects to target stressed individuals, and finally proposed that these sounds might even represent a mechanism for plant–plant communication.

We do not question the main results of the study by Khait *et al.* [2], and we recognize it as an interesting technological improvement that deserves the interest it has generated, even outside the plant biologist community. However, scientists involved in the study of plant hydraulics (as we are) somehow saw in their study a rediscovery of the pioneering work of John Milburn [4] half century ago, who demonstrated that a stressed plant emits sounds (Figure 1). At the same time, we suspect that most of our colleagues were surprised by the lack of references to the large scientific literature on the subject that has not only already described and partly explains all the patterns of acoustic emissions reported by Khait *et al.* [2], but also suggests some possible practical applications.

In this Opinion, we offer an historical perspective on the study of acoustic emissions by plants to better contextualize the significance of recent findings (Figure 2). At the same time, we remind

[1]Dipartimento di Scienze della Vita, Università di Trieste, Via L. Giorgieri 10, 34127 Trieste, Italy
[2]Université Clermont-Auvergne, INRAE, PIAF, Clermont-Ferrand 63000, France
[3]Department of Botany, University of Innsbruck, 6020 Innsbruck, Austria

*Correspondence: nardini@units.it (A. Nardini).

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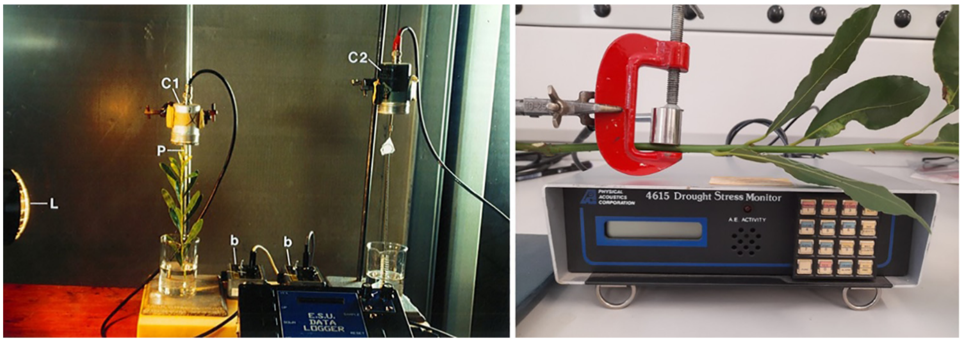

Figure 1. Original set-ups for measuring acoustic emissions. (Left) A refined version of the original apparatus used by Milburn and Johnson [6]. A wire probe (P) was inserted into the xylem of a plant stem and xylem cavitation events were recorded as audible acoustic emissions (AAEs) on Channel 1 (C1). Channel 2 (C2) was a control counter to detect eventual environmental noise. Electromagnetic transducers were located in the metal jars in C1 and C2. The transducers converted the audio signals from the plant into electronic signals (b) recorded by a data logger, differently from the original set-up, where John Milburn was listening and counting AAEs using ear phones [6]. Photograph reproduced courtesy of Williamson [4]. (Right) An apparatus for the measurement of ultrasonic acoustic emissions (UAEs), widely used by several researchers since 1990. The UAE cylindrical transducer was placed in contact with exposed wood after debarking a small portion of stem surface. The transducer converted UAEs into electronic signals recorded by a data logger. The apparatus was designed and tested by Tyree and Sperry [27], and then commercialized as a model 4615 Drought Stress Monitor by Physical Acoustics Corporation (Princeton, NJ, USA).

Glossary

Audible acoustic emissions (AAEs): acoustic emissions in the audible range (20–20 000 Hz).

Ultrasonic acoustic emissions (UAEs): acoustic emissions in the ultrasonic range (>20 000 Hz).

Xylem cavitation: rupture of the water column when under excessive tension (i.e., negative hydrostatic pressure) in the xylem conduits, resulting in xylem embolism. Genuine cavitation events are improbable in plants, where embolism is caused by 'air-seeding' through intervessel pit membranes. The term 'xylem cavitation' is maintained here due to its historical usage in the classical literature on plant hydraulics.

Xylem embolism: gas phase generating and propagating in xylem conduits of plants under drought stress, blocking liquid water transport from roots to leaves and potentially leading to plant desiccation and death.

young scientists that sometimes the answers to our questions can be found in the old literature, often neglected in the modern era of scientific research.

Sounds made by plants: more than 100 years of research and advances

The idea that cavitation events in the xylem can produce acoustic emissions can be traced back to the pioneering work of Henry H. Dixon [5] who conducted experiments with capillary tubes filled with water (or xylem sap collected from *Fagus sylvatica* or *Ilex aquifolium*) heated and then cooled

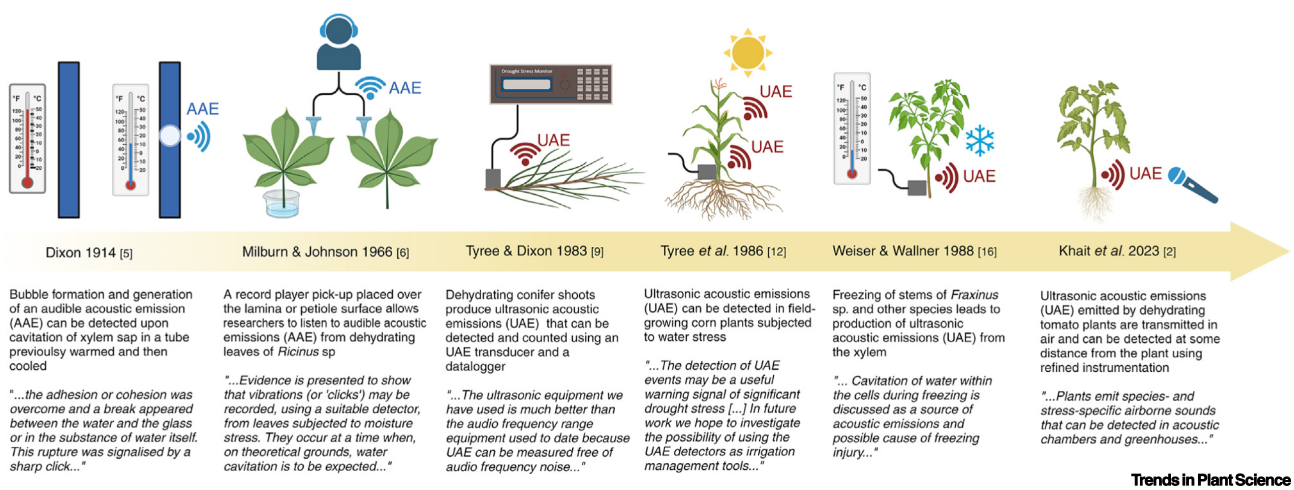

Figure 2. Timeline of the most significant milestones in the study of sound production by plants. The timeline starts with the initial description of audible acoustic emissions (AAEs, in blue) from xylem sap upon cavitation in 1914 [5]. The first recordings of AAE from dehydrating leaves were reported by John Milburn and coworkers [6], whose efforts paved the way to the discovery of ultrasonic acoustic emissions (UAEs, in red) produced by xylem cavitation events from dehydrating plants in the lab and in the field, as well as from plants exposed to freezing stress [9,12,16]. The last piece of the puzzle is the recent discovery that acoustic emissions from plants propagate in air and can be recorded at some distance from the plant surface [2]. Figure created with BioRender (biorender.com).

(Figure 1). Dixon reported that 'As cooling proceeded the tension grew greater and greater, till at last either the adhesion or cohesion was overcome and a break appeared between the water and the glass or in the substance of water itself. This rupture was signalized by a sharp click, and a bubble sprang into existence, which rapidly augmented in size as the water, now relieved from the stretching forces, assumed a volume corresponding to its temperature at the moment'. More than 50 years after the experiments by Dixon, Milburn, and Johnson [6] were the first to demonstrate sound production by plants, by recording **audible acoustic emissions (AAEs)** from *Ricinus* sp. petioles and leaves as well as from several other plant species, and even from fern sporangia. They provided evidence for the correlation between sound emissions and the water status of plant tissues and suggested that AAEs were produced upon cavitation events in water columns under tension in xylem conduits. This original work was extended by Milburn and others [7–11], leading to the discovery of UAEs by plants (Figure 1) and providing an impressive body of evidence supporting the acoustic technique for the detection of **xylem cavitation** in many plant species, paving the way for the application of this technique for field monitoring of plant water status [12–15]. UAEs are transmitted well in solids and liquids, while attenuation in air is high. Thus, placing UAE sensors directly on plant tissues reduces background noise and enables improved detection of the low energy emissions from plants compared with monitoring of AAEs (Figure 2). It was also soon realized that even other stress factors might induce sound production by plants by provoking xylem cavitation. This is the case of not only freezing stress [16–21] (Figure 1), but also some pathological processes [22,23].

Understanding xylem cavitation and sound production by plants

It is likely that cavitation events in the xylem conduits were also the source of ultrasonic signals emitted by tomato and other plants in the experiments reported by Khait *et al.* [2]. These authors were able to record these signals at some distance from the plant by improving the detection and amplification systems compared with those used for the original detection of the same signals with sensors placed in contact with the plant surface. However, the mechanism of xylem cavitation and resulting **xylem embolism** formation as described by Khait *et al.* [2] and Waqas *et al.* [1] is not fully consistent with the current understanding of plant hydraulics. Plants are unavoidably exposed to high water tension (i.e., low water potentials), depending on soil and gravitational potential and, under transpirational conditions, on the water potential of the atmosphere as well as hydraulic resistance in the plant [24]. According to the Cohesion-Tension Theory [25], plants can maintain continuous water columns in their transport system despite substantial negative water potentials; however, at specific vulnerability thresholds, 'air seeding' can lead to the entry of air, most likely via interconduit pit membranes [26]. This causes a sudden rupture of water columns and a consequent sudden release of tension, which results in vibrating cell walls and generation of sonic waves [27,28]. Accordingly, strong acoustic signals can be registered when the water potential in the cavitating conduit is low, the conduit is large (and, thus, there is more energy stored), and attenuation on the way to the sensor is low. In affected conduits, gas bubbles expand and any remaining water evaporates, while pit structures isolate the embolized conduit from adjacent, functional ones [29–31]. There is no flow of small bubbles through the xylem because of: (i) this isolation effect; (ii) the fact that any small bubble would induce another cavitation event; and finally (iii) the fact that most plants downregulate transpiration at critical water potentials to prevent runaway xylem cavitation [32,33]. Figure 1 of Waqas *et al.* [1] (and the cover of the 2023 September issue of *Trends in Plant Science*) is misleading in this aspect. The xylem transport system also reaches from the fine roots to the highest order veins of leaves; thus, stems may not be the only source of UAEs [34,35].

Xylem cavitation can also be caused by freeze–thaw events, and several studies demonstrated UAE production related to this process in both conifers [19,20,36] and angiosperms [16–18,37].

According to the 'thaw-expansion hypothesis' or 'bubble formation hypothesis' [38–41], gas bubbles are formed during freezing because air is soluble in the liquid but not in the frozen xylem sap. During thawing, these bubbles can redissolve in the surrounding sap; however, when the water potential of the xylem sap is low and bubbles are large, they may expand and block the respective conduit [41]. Hence, large vessels (e.g., of ring-porous species), which contain a lot of dissolved air and, thus, form large bubbles in ice, are at high risk of freeze–thaw-induced cavitation [42]; this risk is highest when freeze–thaw events are combined with drought stress [41]. UAEs were demonstrated to occur during ice formation, indicating that bubble formation releases tension just before the sap freezes [18,19,43].

Patterns of sound production by plants

Several of the experimental observations and patterns of UAEs described by Khait *et al.* [2] are well known and already partly explained. For example, diurnal patterns of UAEs corresponding to stomatal kinetics have been already described, and are consistent with current understanding of correlations between transpiration rate, water potential drop, cavitation events, and stomatal closure to control and prevent runaway cavitation throughout the xylem system [12,44–46]. The observation that cut stems produced more UAEs in a shorter time interval compared with intact drying plants is also fully consistent with current knowledge of the effects of 'open conduits' as air sources facilitating air-seeding and embolism propagation in the xylem system [47], leading to artefacts in quantification of vulnerability thresholds [48]. Even the observations that variable sound frequencies from different plant species might correlate with xylem conduit dimensions is not novel, given that Ritman and Milburn [10] had already postulated such a correlation, which was later confirmed by Ponomarenko *et al.* [28]. Recent studies provided additional insights into the origin of variable sound frequencies from dehydrating stems [49]. Indeed, plant stems are very heterogeneous media for sound propagation [50], which varies for air (embolized conduits), water (xylem sap), and solid materials (cell walls). Sound waves are likely influenced by all these factors, leading to complex sound conduction and attenuation effects [51]. In this respect, it is not surprising that Khait *et al.* could not detect any airborne sound in the only two woody species analyzed [2]. In fact, in woody plants, the presence of a secondary bark likely attenuates any UAEs produced by stems to a level not compatible with the sensitivity of the recording apparatus placed at some distance from the plant surface. Not surprisingly, even detecting UAEs from woody stems using sensors placed in contact with the plant surface often requires preliminary removal of a small portion of bark [31,51].

Not only xylem cavitation: other known sources of sounds from plants

In their commentary [3], Hussain *et al.* discuss the possibility that not all the sounds recorded by Kaith *et al.* [2] originated with xylem cavitation events. Indeed, this was already clear to John Milburn, who suggested that snapping of fibers, breakage of cell–cell connections, or crushing and shrinking of cell walls might all be responsible for sound production by plant tissues [6,10,49]. More recently, Rosner *et al.* [52] showed that some UAEs could be produced by the formation of radial cracks in dehydrating wood undergoing progressive shrinkage [53,54]. Lamacque *et al.* [55] reported that lavender plants undergoing dehydration produced two very distinct phases of UAEs, the first associated with a significant increase in loss of xylem conductance due to embolism formation and build-up, and the second associated with a significant increase in cellular damage, likely coupled with membrane rupture, intracellular cavitation, and cell wall shrinkage and cracks. Scientists inclined to an anthropomorphic view of plant functioning (which we are not) might then conclude that plants 'cry for help' when they face drought, and then 'cry for desperation' when they are facing death by cellular damage.

Is there anybody out there listening to plant sounds?

The joke proposed at the end of the previous section leads us to some final considerations about the possible functional roles of sounds emitted by plants facing drought stress. As we have

Outstanding questions

Are airborne acoustic emissions useful for field detection of the level of drought stress suffered by plants, and are they more practical and/or informative compared with remote detection of other parameters, such as leaf water content or leaf surface temperature, which is routine science nowadays?

Can we easily separate acoustic emissions produced by plants upon xylem cavitation from those arising from terminal stages of dehydration, such as cell wall shrinking or membrane rupture?

Do we sufficiently understand the processes of sound formation and transduction in plants for reliable interpretation of acoustic emissions, especially in the field?

Do sounds emitted by plants provide any significant information to insects feeding on stressed plants, and can we undoubtedly demonstrate that insects indeed target plants based on sounds produced by xylem cavitation events?

How can we transmit to younger generations of scientists the need to closely scrutinize old literature for studies that have already described and explained supposedly novel experimental observations?

detailed, AAEs and UAEs are produced by pure physical processes related to the structure of xylem and to the mechanism of sap ascent based on negative hydrostatic pressures. Hence, there is no known active physiological process allowing plants to produce UAEs and transmit them to the surrounding environment. Nonetheless, it is not impossible, in principle, that some organisms, namely herbivores and especially insects, might be able to detect these acoustic waves and use them to select plant individuals facing stress conditions, as already suggested (but not demonstrated) by Haack *et al.* [56]. We acknowledge that such a demonstration would be highly novel, but the study by Khait *et al.* [2] does not report any experiment to test this possibility. While some reports have suggested that plants are able to detect sounds generated by insects and other sources [57], we are not aware of experiments supporting the hypothesis that sounds produced by plants are somehow informative for insects [58,59]. Indeed, it is likely that insects interested in using plant-emitted UAEs to target their feeding behavior would face the same problem tackled by researchers trying to detect these signals in the open field (i.e., pervasive background noise in the same frequency range). There are several other physical and chemical signals emitted by plants under stress that could serve much better for this purpose. As an example, drought-stressed plants close their stomata to reduce transpiration (and avoid xylem cavitation), and this causes a significant increase of leaf temperature due to the lack of the evaporative cooling effect. Distinguishing healthy and drought-stressed plants in the field is much easier even for scientists when using instruments designed to measure leaf surface temperature [60], rather than listening to sounds produced by xylem cavitation (see Outstanding questions).

Plants emit sounds, but this does not necessarily mean that somebody is listening to them or is even interested in what they have to say. Even our joints produce acoustic emissions, and this is especially true for those of us well over our 50s. As an example, knees produce acoustic emissions that orthopedics can use as biomarkers for a quantitative assessment of joint aging and degeneration [31,61], just like plant physiologists can use plant-emitted UAEs to assess the occurrence of drought stress. Then the question is: when we hike or run in the forest, shall we worry about predators outside listening to acoustic emissions from our knees to identify an older human for an easy dinner? Possible, in principle, but still awaiting experimental demonstration.

Declaration of interests

No interests are declared.

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