Trends in
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Plants can talk: a new era in plant acoustics

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Plants release chemical signals to interact with their environment when exposed to stress. Khait and colleagues unveiled that plants 'verbalize' stress by emitting airborne sounds. These can train machine learning models to identify plant stressors. This unlocks a new path in plant-environment interactions research with multiple possibilities for future applications.

Plants interact with one another and their surroundings through physical and chemical cues. Upon exposure to biotic and abiotic stress, plants release certain analytes in their root exudates as well as volatile organic compounds (VOCs) in the air to interact with neighboring plants and trigger resistance to stressors therein [1]. In addition, stressed plants can also produce chemical cues that lure beneficial microbes or natural predators to insect herbivores to aid both themselves and their neighbors [2–4]. The various ways in which plants interact with their surroundings has attracted worldwide scientific attention. Emerging from this global interest to deeply understand the subject, the 'plant bioacoustics' hypothesis posits that plant–ecosystem interactions are also controlled by sound and that crop health can be significantly improved by tracking such plant-emitted sound cues. However, information about the ability of plants to emit stress-related acoustic cues has remained enigmatic.

Research by Khait *et al*. unveils that plants effectively produce sounds when they are stressed and they continually exchange information about their own survival and development via cryptic noises [5]. The authors discovered that tomato (*Solanum lycopersicum*) and tobacco (*Nicotiana tabacum*) plants placed inside an acoustically isolated environment produced more sounds than the control group when watering was withheld for several days, or when subjected to stem cutting. Their investigation demonstrates that plants can emit popping or clicking sounds at frequencies between 20 and 100 kHz. To verify the proof-of-concept design, Khait *et al.* further elegantly demonstrated that distinct plant species and stress situations can be classified based on the emitted sounds, using trained machine learning models (support vector machine classifier with scattering network) with a high accuracy of more than 70% (Figure 1A). These findings suggest the potential of using plant airborne acoustic cues as a stress marker in agricultural production.

Previous studies have shown that plants can respond to sounds and that sound waves may enhance their ability to withstand drought, raise their resistance to diseases, and increase agricultural yields [6]. Environmental sounds of biotic and abiotic origin not only cause plants to undergo biochemical and molecular changes [6], but they may also induce shifts in the structure of the plant-associated microbiome [7]. Additionally, there is startling proof that sounds produced by insects (e.g., caterpillars' chewing) sparked protective reactions in plant leaves [8]. Interestingly, Khait *et al.* hypothesized that plant-emitted sound can also be detected by certain mammals and insects from a distance of 3–5 m. These acoustic cues are emitted not only by tobacco and tomato plants, but also by wheat, corn, grapevine, cactus, and henbit. The unique sounds emitted by different plants could have important ecological and evolutionary implications for the plant communities.

Water availability has a substantial impact on plant phenology processes and is becoming more important as a consequence of climate change and variations in regional water supplies. Khait *et al.* found that, with less available water, plants begin to produce more sounds compared with the irrigated ones, which peak on the fifth day of drought; thereafter, the plants wilt and sound diminishes. A significant positive association was found between the hourly sound frequency and the transpiration rate of plants. In addition, Khait *et al.* reported that tomato plants emit sounds when infected with the tobacco mosaic virus (TMV). However, the mechanistic insights into how plants emit sound remain unclear. Several possibilities can be envisaged. Earlier studies have shown that clicking and popping sounds emanating from plants may be the result of bubbles bursting inside the plant's vascular tissues [6]. One piece of supporting evidence provided by Khait *et al.* includes the observation that the sound frequencies of plants with larger trachea diameters are lower and that sounds released by trachea spread in all directions from the stem. However, the trachea being comparable with tubes, the length of the vessels may also influence the produced frequencies, much like the relation between the tube length of wind instruments and the pitch of sound produced. Although the underlying mechanisms by which plants emit airborne sounds are still unclear, this work effectively sheds light on the use of machine-learning models to distinguish different forms of stress based on the plant-emitted sounds and their promising role in the advancement of precision agriculture. Most importantly, these intriguing findings set the stage for resolving critical ecological questions in relation to plant acoustics.

Open questions for future research

Since the findings of Khait *et al.* have uncovered that stressed plants can produce airborne sounds, future studies on plant

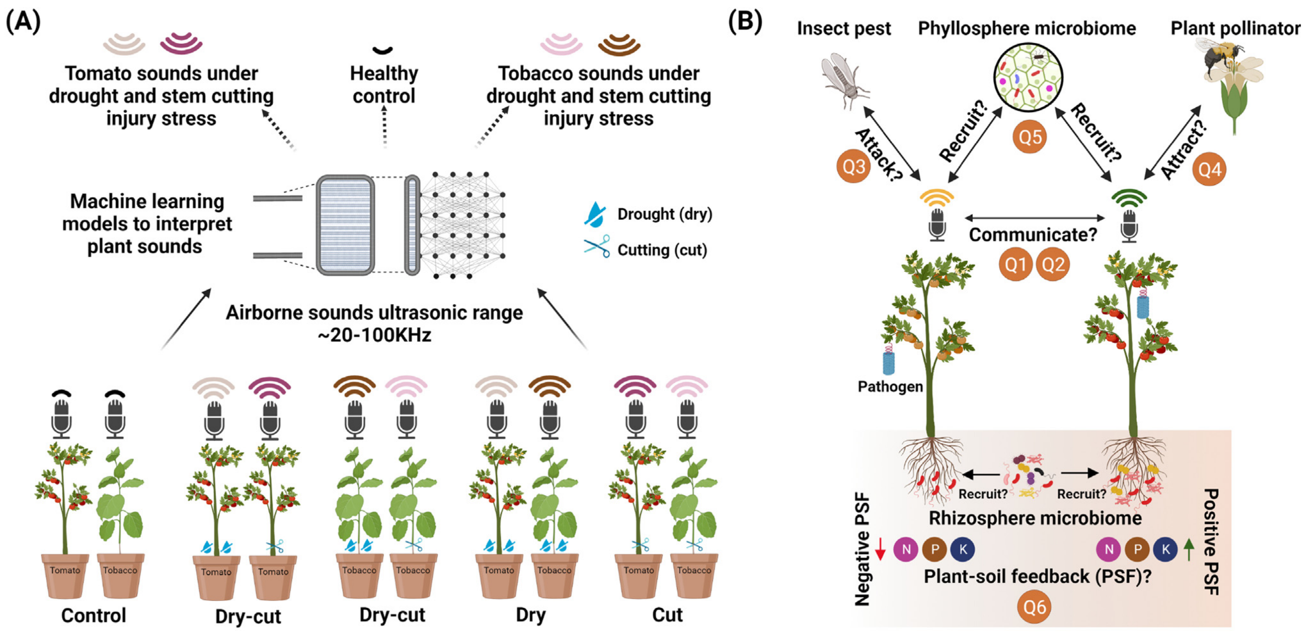

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Figure 1. Plants emit distinguishable airborne sounds in response to varied stress situations, with unclear implications for the biological diversity around them. (A) Tomato and tobacco plants were subjected to a variety of stressors, including drought stress (dry; tomato and tobacco) and stem cutting (cut; tomato and tobacco). Plants exposed to these stressors emitted airborne ultrasounds with frequencies ranging from ~20 to 100 KHz. Machine learning models were trained using these recordings to identify tomato and tobacco plants experiencing drought and cutting stress. Through informative airborne sound cues, four tomato and tobacco stress scenarios (tomato-dry vs. tomato-cut, tobacco-dry vs. tobacco-cut, tomato-dry vs. tobacco-dry and tomato-cut vs. tobacco-cut) were effectively monitored with ~70% accuracy. Different color of sound waves represents the specific frequencies associated with various plant species and stress conditions. (B) It is unclear whether plants 'talking' through airborne sounds during times of stress may induce changes in response of other biological organisms, such as neighbor plants (Q1, Q2), insects (Q3, Q4), the rhizosphere and phyllosphere microbiome to combat pathogens (e.g., viruses) (Q5), as well as produce acoustic sounds in both positive and negative plant–soil feedback (PSF) conditions (Q6), illustrated on the right-hand side (see open questions for future research for detail). Images created with BioRender (www.BioRender.com).

bioacoustics must include ecological and molecular perspectives, taking into account intra- and interspecific plant interactions, interkingdom interactions (plants, animals, and microbiomes) and plant–soil feedback (PSF) to deeply understand the secret language of plants in ecosystem interactions [9]. We have listed and discussed key research questions below.

1. What are the different mechanisms of sound production by plants? One of the primary questions is how plants produce sounds. Plants are known to emit sounds involuntarily through cavitation [6]. While Khait *et al.* propose cavitation as one of the mechanisms of sound production, they noted only a partial overlap between the cavitation and the recorded sound frequencies; hence, leaving the door open for future research. The frequencies that were recorded but not linked to cavitation, could correspond to altered water relations within the plant tissue. Earlier work on *Ulmus glabra* also indicated that the significant variability in spectral frequency and waveforms of the acoustic cues under transpiration and rehydration cannot be adequately explained by cavitation [10]. Thus, identification of other modes of sound production would further strengthen the hypothesis of sound-based plant–plant interactions.
2. Do plants interact bidirectionally through acoustics? Further to the considerations under key question 1, it is important to consider directionality of information exchange. Indeed, research on the mechanisms of sound production showing that these have evolved to produce sound and are not an incidental by-product of physiological processes, as well as experiments demonstrating that receivers respond to those sounds in ways that benefit the emitter, is needed to understand whether in the plant kingdom, sounds act as unintended cues rather than signals, shaped by natural selection because of their influence on receivers. With massive experimentation, Khait *et al.* showed that plants do emit sounds, especially when they are stressed; however, it is unclear whether such acoustic emissions form the basis of plant–plant interactions (i.e., whether this is uni- or bidirectional). Indeed, plants have been shown to exhibit plasticity in response to airborne chemical signals emitted from stressed plants [11], indicating the existence of

bidirectional information exchange. Yet it remains unclear whether neighboring plants can detect, echo, or amplify the signal in reply to acoustic cues received from stressed plants. In this regard, it is important to note that discovery of other mechanisms of sound production, different from cavitation, is awaited. Irrespectively, designing and carrying out bioacoustics functional experiments, including diverse host plant species and varying levels of (a)biotic stress, may aid in deciphering whether acoustic interactions between plants are bidirectional.

3. How do insect pests react to the airborne sound cues that stressed plants emit? According to Khait *et al*., insects within a distance of 3–5 m may detect the sounds that stressed plants emit. It is worth noting that stressed plants are more susceptible to insect herbivores [12]. Consequently, it is conceivable that insects may assess plant health by eavesdropping on airborne sounds emitted by plants, thus determining when to invade them. There also exists a possibility that such sounds may allure natural predators to ward off these pests, like has been reported in VOC-mediated tri-trophic interactions [4]. Screening the influence of recorded plant sounds on host insect pests to track precise changes in their expression profile using 'omics' approaches can be valuable to identify whether insect pests can respond to plant sounds.
4. Do airborne sounds produced by plants affect plant–pollinator interactions? Insects have long been known to produce sounds and studies have shown that the sound of bees buzzing can enhance the sweetness in floral nectar, besides resulting in the vibrational dehiscence of anthers, facilitating pollination [13]. Moreover, insects that live on plant parts and communicate through substrate-borne vibrations may be profoundly affected by the vibrations caused at the plant surface upon acoustic emissions [14]. The potential for plants to react to sounds produced by insects, as well as their ability to emit acoustic cues themselves, suggests that sound may serve as a mode of plant–pollinator communication. Studies should include both plant and insect pollinator sounds to provide mechanistic insights into the uniqueness of plant–pollinator interactions. Screening for 'deaf' plant mutants could present a first entry to unravel the molecular mechanism involved.
5. Do airborne sound cues from pathogen-infected plants affect the plant microbiome? Khait *et al.* have demonstrated that tomato plants emit sound when infected with TMV. Earlier studies have revealed that when pathogens attack a plant, they recruit specific microorganisms for disease suppression [2]. It is important to note that grapevine that was continuously exposed to sound vibrations had a distinct phyllosphere microbial community composition compared with a non-exposed control group [7]. Building on this, we hypothesize that the airborne informative sound cues from stressed individuals may aid in recruiting a specific subset of microbes that strengthens the plant's resistance to pathogen infection (Figure 1B). Integrative methods that combine plant bioacoustics experiments with microbial community amplicon sequencing, shotgun metagenomics, targeted microbial cultivation, and thus screening for alterations in the rhizosphere and phyllosphere microbial communities upon pathogen attack may reveal a link between plant sounds and microbiome recruitment for disease protection.
6. Do plant sounds influence PSF? As plants grow, they alter the nutrient availability and soil biota that can be significantly correlated with plant growth and survival (PSF), affecting plant community dynamics. Khait *et al*. successfully mapped and differentiated plant sound under drought and injury stress; however, it is unclear whether plants similarly emit sounds of different frequencies under both positive and negative PSF conditions. Evidence suggests that drought has long-lasting effects on soil microbial communities with stronger implications for PSF and plant–plant interactions [15]. Experiments, wherein the soil environment is changed by adding or removing nutrients, altering the soil pH, or inoculating soils with plant-beneficial and -suppressive microbial communities, could shed light on this.

The ability to emit and perceive acoustic cues could play an important role in the plant kingdom. Considering the critical questions mentioned earlier and testing hypotheses will enable us to gain a holistic view of acoustics-based communications in plant life (Figure 1B). Fine mapping and registration of plant species-specific sounds under varied environments, combined with remote imaging technology [9], may enable the rapid identification of biotic and abiotic stressors, improve water and nutrient use efficiency, and reduce fertilizer and pesticide application, thereby increasing horticulture and agronomic crop productivity. As plant acoustic research moves into the field, its value and integration in agricultural settings for the upcoming generation of healthy crops await careful assessment in agroecosystems.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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