

Bearing Fruit: Plant Bioacoustics is Blossoming

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There is growing interest in how plants transmit, reflect, generate, and perhaps even respond to sound.

Plants comprise about 80% of the Earth's biomass and capture over 100 billion tons of carbon per year in additional biomass. They form the foundation of the animal kingdom's food supply; transform our atmosphere; loom over our art, agriculture, and architecture; and inspire work in many scientific disciplines, from genomics to biochemistry to ecology. Yet the role of sound in plant studies has received relatively little study from bioacousticians, remaining a topic more likely found in the realms of urban legend (playing Mozart to your plants) than in peer-reviewed literature.

Indeed, although the Acoustical Society of America (ASA) has an Animal Bioacoustics Technical Committee, nothing is formally organized with respect to plants. However, over the past decade, interest in the relationship between sound and plants has begun to, well, sprout. Over the past two decades, nearly 200 publications on the subject have appeared.

In May 2018, the ASA hosted an exploratory special session on plant bioacoustics that attempted to survey the many ways the field of acoustics intersects with fields of plants. This article germinated from that session, which explored four different topics relating acoustics to plants.

This article begins with reviewing how plants distort and transmit sounds generated by insect pests and then examines some surprising examples of how plants have evolved to reflect and enhance animal sounds, potentially opening new facets in animal-plant interaction studies. The focus then shifts to how plants can generate sounds through photosynthesis and transpiration stress, reviving long-standing interests in using non-invasive passive acoustics to diagnose and measure plant physiology.

Finally, the discussion branches into more speculative territory, as a relatively recent spate of publications suggest that plants can sense and respond to acoustic and mechanical stimuli, despite the fact that these organisms lack an identifiable nervous system.

Stem Seismology: How Pest Sounds Disperse in Vegetation

Bioacoustic studies of insect pests have provided the longest paper trail for bioacoustic plant studies, with papers on the topic of detecting insect pests first appearing in 1909, with a description of the sounds of termites chewing wood (Main, 1909). A few papers per decade then dribbled through the literature during the twentieth century, but over the past 30 years, there has been a substantial jump in literature (132 articles/patents up to 2011) on detecting the presence of agricultural pests on both living and harvested plant material, which is a topic of intense agricultural, economic, and environmental interest. Like many acoustic subdisciplines, this advancement in interest can be directly related to the falling costs of hardware

to detect and measure sound and the increasing sophistication of computational signal-processing abilities. Studies using bioacoustic tools to detect plant-based pests will continue to expand, given that over 218 species across 12 different insect orders have been identified as using sounds or vibration for communication, with the true number of species certainly being much higher (Hill, 2008).

Investigators across the United States study a wide variety of pests. Richard Mankin at the US Department of Agriculture (USDA) has conducted research on how to spot invasive pests like the devastating Asian citrus “jumping plant lice” (*Diaphorina citri*) and Asian longhorn beetle (*Anoplophora glabripennis*) in living trees, whose larvae break fibers while feeding or moving through woody tunnels (Mankin et al., 2011, 2018). Alexander Sutin at the Stevens Institute of Technology (Hoboken, NJ) has focused on insect detection in agricultural shipments and wood packing materials (Sutin et al., 2017). Richard Hofstetter at Arizona State University (Tempe) has conducted detailed investigations into the sounds of multiple species of piñon bark beetles, which naturally live in native piñon trees throughout the American West (Hofstetter et al., 2014). However, a drying climate has stressed these trees, leading to outbreaks of bark beetle infestations that have been estimated to kill nearly a third of piñon trees in the United States.

Despite the wide variety of species examined, there are consistent patterns and challenges faced by all these researchers. Many insect larvae in woody substrates produce broadband, even ultrasonic, pulse trains of short, 1- to 10-ms impulses. The pulses often occur in short bursts, with interpulse intervals of 200 ms or less. Adults of other species generate tonal signals with substantial harmonics. The signals are normally detectable to only several centimeter ranges when propagating through the air, but whenever the vibrations of a single animal travel through plant substrates, they have been detected by accelerometers up to 4 meters distant before fading into the background noise spectrum. Ultrasonic sounds (>20 kHz) are particularly effective for long-range detection because background noise levels are generally low.

The increasing scrutiny of these sounds has made plant researchers appreciate how crucial the structure of plants is in transmitting and modifying sound. The anisotropic and heterogeneous nature of plants causes filtering, waveguide dispersion, and even the resonant enhancement of insect signals

in a manner that a seismologist or ocean acoustician would find familiar.

Lujo et al. (2016) have presented in detail one example of such research in plant lice. Males vibrate their wings to generate 0.2-kHz tonal signals with harmonics up to 3 kHz, which are transmitted down their legs into tree branches. The relative strength of these harmonics changes with distance along a branch, but females tend to respond as long as a few harmonics are still present. Waveguide dispersion effects are apparent, with different frequency components traveling at different speeds along the branch, and multiple researchers have speculated that insects might exploit these frequency-dependent absorption and dispersion effects to estimate the direction and distance to a potential mate.

Even more intriguing is the limited evidence that suggests that insect sounds can be transmitted *between* different plants, even those that aren't physically touching. Shira Gordon and her colleagues at the USDA (2019) have investigated how mating calls from the glassy-winged sharpshooter (*Homalodisca vitripennis*) are transmitted through grapevines by using a transducer to mechanically vibrate a single plant stem and then using a laser Doppler vibrometer (LDV) to characterize the resulting transmission along the plant. Like other researchers, Gordon et al. found evidence of frequency-dependent dispersion, in that the higher harmonics of the call had higher group sound velocities than the lower harmonics, consistent with Bernoulli-Euler beam flexure theory. What was more surprising was that they found evidence that these artificially generated calls could be transferred between nonconnected plants by sound radiation from the broad grape leaves that act like crude diaphragms in speakers. The LDV could still detect 100-Hz vibrations on plants separated by up to 10 cm from another plant agitated by the transducer, albeit attenuated by 60 dB, with higher frequency components detectable at shorter distances.

The practical importance of plant propagation effects on insect signals is that it complicates efforts to automatically detect and distinguish insect sounds from other acoustic sources, a problem familiar to many animal bioacousticians. Furthermore, researchers are investigating whether acoustic playbacks of insect sounds or variations thereof could be used to prevent or even expel existing pests from trees using various sounds (e.g., Hofstetter et al., 2014), and knowledge of the transmission path through plants is an obvious requirement for reproducing convincing fidelity.

Who's Signaling Who? Animal-Plant Acoustic Interactions

Given that plants play such an important role in transmitting animal signals, biologists have begun investigating whether plants have evolved mechanisms to enhance or repress animal acoustic signals. Although current evidence is fragmentary, what exists is intriguing. During a presentation at the ASA plant bioacoustics special session, Michael G. Schöner at the University of Greifswald (Greifswald, Germany) revealed that various bat species pollinate around 250 genera of tropical plants. His close examination of several of these species has found that the petals and flowers of these plants generate strong reflections of bat ultrasonic signals over a broad range of aspect angles. Removal of these structures reduced the ability of bats to locate and pollinate the plants (Schöner et al., 2016). As one particular example (Figure 1), a pitcher plant (*Nepenthes hemsleyana*) that serves as the mutualistic (mutually beneficial) host for a small bat species (whose feces fertilize the plant) has a concave structure in the back wall that serves as a reflector. A closely related pitcher plant species that does not host bats lacks this structure and is dramatically less acoustically reflective. Although these detailed measurements have been directly conducted only in a few plants, Schöner et al. noted that the fertilization by bat feces is not uncommon in other plant species, including trees. They also observed that many bat-interacting plants display *flagellichory*, the characteristic of exposing fruits by hanging them on a long peduncle, a structure would seem to enhance a bat's ability to acoustically detect fruit.

Although his research has been confined to bats, Schöner et al. (2016) have speculated whether plants have evolved structures to enhance signals from other animal orders such as insects. Several ant species colonize plants and have alarm signals that are transmitted via knocking their bodies on the plant's stem, alerting the entire colony. No one knows whether plants could have evolved efficient means of enhancing these signals.

However, entomologists have studied the phenomenon of "buzz-pollination" for decades, wherein pollinating insects (mostly bees) use vibrations to release and extract pollen from flowers. Buzz-pollinated flowers occur in species from 65 different plant families and are believed to have independently evolved multiple times. Although considerable research has examined the behavior and signals produced by pollinating insects, a recent review paper on buzz-pollination (De Luca and Vallejo-Marin, 2013) noted relatively little work has been performed on how the mechanical structures of flowers

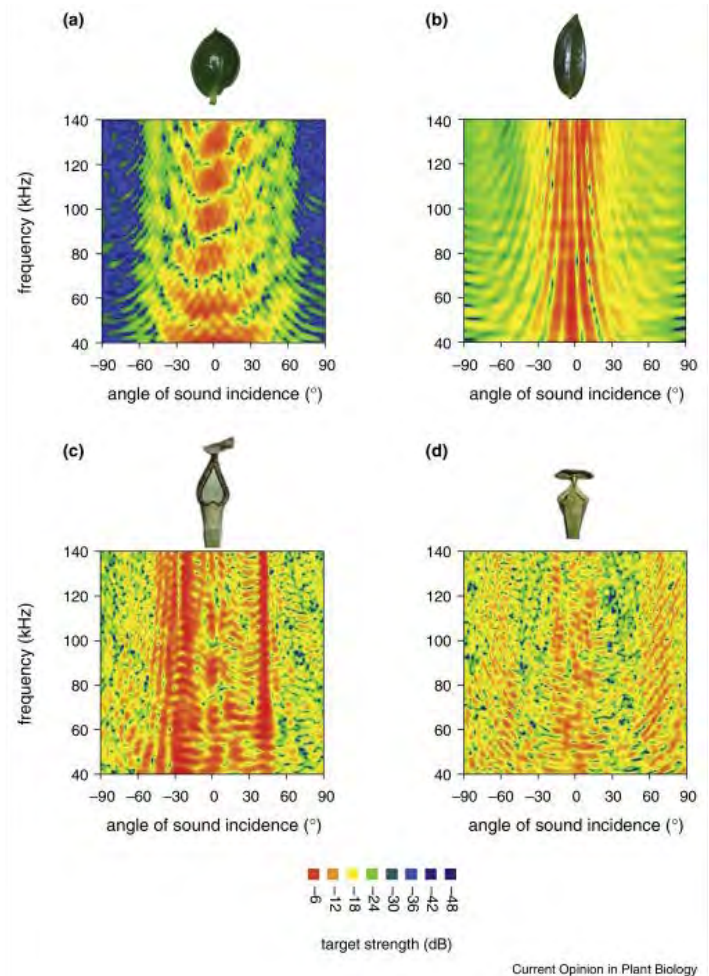


Figure 1. Passive acoustic signaling in two nonrelated plant species. The neotropical vine *Marcgravia evenia* attracts bats, which pollinate its flowers. Exemplary spectral directional patterns of a dish-shaped leaf (a) and a foliage leaf (b) are shown. Dish-shaped leaf echoes were of high intensity, were multidirectional, and had an invariant echo signature compared with those of foliage leaves. The paleotropical carnivorous plant *Nepenthes hemsleyana* attracts bats that fertilize the plant with their feces. Exemplary spectral directional patterns of the back wall of *N. hemsleyana* pitchers (c) show that this structure is a similar multidirectional echo reflector as the dish-shaped leaves of *M. evenia*. Such structures are missing in other pitcher plant species such as *N. rafflesiana* (d), the closest relative of *N. hemsleyana*, that does not attract and host bats. Reprinted from Schöner et al., 2016, with permission from Elsevier.

may have coevolved to permit species-specific stimulation of pollen release.

Perhaps further surprising acoustic interactions between plants and animals lie in wait.

Probing Plant Physiology

Plants can transmit and reflect animal sounds, but they also produce sounds as well as a result of various physiological processes. Bending and drying wood produces microfractures and other displacements that can generate acoustic energy, a process dubbed acoustic emission (AE). As far back as 1933, Kishinouye (1990) conducted what may have been the first AE experiment by recording the sounds made by a piece of wood under bending stress. Active research continues into using AE techniques to check the quality of lumber being dried on an industrial scale as well as being a host of other inorganic structures and materials.

However, the most consistent acoustic study of plant physiology began in 1966 (Milburn and Johnson, 1966), when researchers observed that dehydrating plants produce ultrasonic cavitation sounds. We all know that plants need water to survive, but what we generally do not realize is that less than 1% of the water consumed by a plant is used to grow via photosynthesis.

Instead, more than 99% of the water absorbed by plant roots rises through the stem or trunk along a thin cylindrical layer called the *xylem*, on its way to being transported toward *stomata* embedded in the leaves where it eventually transpires into the atmosphere. This internal water flow transports nutrients to the leaves and cools and maintains the shape and structure of the plant on both a macro- and microscopic level. As the water evaporates from the leaves, the high viscosity (and thus surface tension) of the water causes it to be wicked up from the roots, and thus the various conduits conducting water through the xylem are under hydraulic pressure. When water becomes scarce in the ground, the conduit tension increases, just like the tension you feel in your mouth when trying to suck a particularly thick milkshake through a small-diameter straw. When the milkshake is nearly gone, air bubbles enter the straw and create loud sounds that siblings have used to annoy each other for generations.

Similarly, if the hydraulic tension in the xylem of the plant gets too large, gas will begin entering the conduits, forming cavitation bubbles that, if they grow too numerous and large, will impair sap flow and eventually wilt and kill the plant. As these bubbles form and cavitate, they radiate acoustic energy, as any frustrated underwater propeller engineer will tell you. These ultrasonic signals can be picked up by transducers placed in the bark and can thus reveal whether an in situ plant is drought stressed.

The possibility of using noninvasive, nondestructive acoustic methods to measure the drought stress of plants in the field has fascinated scientists for decades. This is because standard methods for measuring hydraulic conductivity involve needles and other invasive poky things, which tend to inject air bubbles, creating all sorts of artifacts in the resulting measurements.

However, multiple challenges face acoustic measurements. Plants produce bubbles in a multitude of ways beyond dehydration, including fiber cavitation, mechanical strain and fracturing, rewatering, freezing, and thawing. Progress on this front has interesting parallels to signal classification in animal bioacoustics; increasing signal-processing capabilities has allowed more detailed features of cavitation signals to be extracted and correlated with different source mechanisms. For example, recent work has found that dehydration cavitation generally produces signals with peak frequencies between 100 and 200 kHz, whereas other bubble-formation processes tend to produce signals with lower peak frequencies (De Roo et al., 2016). Hindering further progress is a lack of knowledge about the detailed micromechanics of how cavitation bubbles form. And just as the case with insect sound transmission, the ultrasonic cavitation signals experience absorption and dispersion as they work their way through the complex structure of a plant, complicating signal feature extraction and classification.

Even more troublesome is that all acoustic metrics to date are nonlinearly related to dehydration level (formally defined as percentage loss of hydraulic conductivity), in part because acoustic cavitation is related to *changes* in air embolism (dehydration) rather than the absolute level of drought stress itself. Raw counting of cavitation signal rates turns out to be an inconsistent indicator of drought stress, so more recent work has added measurements of cumulative energy (or sound exposure), which has led to some improvements (De Roo et al., 2016). The prospect of measuring drought stress in the field with acoustics remains tantalizing.

A completely independent line of research into plant photosynthesis has emerged in underwater acoustics, where multiple researchers have investigated how underwater photosynthesis in seagrass and, more recently, marine algae can be detected using sonar. The work by Freeman et al. (2018) on algae has even found that photosynthesis can be measured with passive acoustics by detecting the “ringing” of the oxygen bubbles as they separate from the plant and drift toward the surface. Tank measurements of

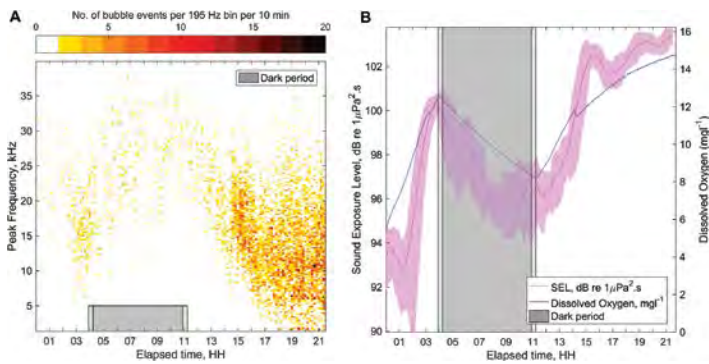


Figure 2. Relationship between algae photosynthesis and passive acoustic bubble detection. **A:** relationship between time of day, bubble detection rate, and bubble frequency. **B:** relationship between measured sound exposure level (SEL) of bubble pulses and dissolved oxygen level in tank. Reproduced from Freeman et al., 2018.

the alga *Gracilaria salicornia* showed that photosynthesis causes bubble oscillations between 3 and 35 kHz, with the cumulative sound energy (sound exposure level) tracking the rising and falling of dissolved oxygen levels across daytime and nighttime light levels (Figure 2).

Interestingly, Freeman et al. (2018) found that field measurements of daytime ambient noise in this same frequency band appear to correlate with the percentage of algal cover on coral reefs, independent of other reef-based bioacoustic processes. Algal dominance is a key indicator of coral reef ecosystems stress because warmer waters, polluting nutrients from terrestrial runoff, and the removal of herbivorous fishes for human consumption all promote algal growth. These observations suggest that it may be possible to quantify the degree of reef degradation through passive acoustic monitoring.

Beatles and Beetles: Do Plants Respond to Sound or Other Vibration?

Despite casual appearances, evidence abounds that vascular plants respond to changes in environmental conditions. Flowers open during the day and close at night, roots grow in the direction of moisture, and leaves generate natural repellents when an insect chews on them. Plants even respond to the actions of other plants via communication by direct touch, light, and chemical compounds. For example, plants near drought-stressed plants will respond by closing the stomata in their leaves so as not to lose more water.

It is not surprising, therefore, that many have wondered whether plants respond to sound or mechanical vibration

over both short- and long-term scales despite their lack of clear sensory mechanisms for detecting it. Trees do change growth patterns in response to low-frequency mechanical vibration. For example, scientific studies of the effect of wind on tree growth go back to 1803, and the impressive (and vaguely Dr. Seussian) term “thigmomorphogenesis” was coined in 1973 to “describe the response of plants to wind and other mechanical perturbations, including mechanical bending or flexing or by touching or brushing by passing animals” (Telewski, 2006, p. 1468). If plants could change growth patterns in response to low-frequency perturbations, why not sound?

The earliest peer-reviewed research on the topic from the 1950s and 1960s seemed focused on how music playbacks influenced plant yields (Klein and Edsall, 1965). There seemed to be little attempt to standardize procedures for music selection, and one can find literature results for Karnatic music (a form of Indian classical music), Gershwin’s “Rhapsody in Blue,” wedding music, Gregorian chant, and the Beatles (specifically, “I Want to Hold your Hand”). There was also little-to-no attempt to standardize species selection, playback duty cycle, source level, or other playback variables, and even definitions of plant response were inconsistent. Given the lack of controls and standardization, one would probably not be shocked to realize that the reported responses were all over the map (e.g., “we could not observe any stem nutation in plants exposed to the Beatles”; Klein and Edsall, 1965) and generally irreproducible. Work on the topic dropped into the realms of urban folklore and middle-school science fair projects. Highly questionable claims by a 1973 bestselling book, *The Secret Lives of Plants*, cast a miasma over the entire topic for decades.

A series of papers by Weinberger and various coauthors (e.g., Weinberger and Burton, 1981) seem to be among the first to eschew music in favor of single-frequency tones and other simple reproducible signals to study plant response. The continuing advent of low-cost electronically customizable and reproducible sound playbacks seems to have led to a spurt of credible research on the topic, with more rigorous controls, beginning in the twenty-first century (Jung et al., 2018).

Several papers have attracted particular attention. Appel and Cocroft (2014) published observations that the playback of caterpillar feeding sounds (think “munching”) in the absence of caterpillars led rosette plants to release higher levels of chemical defenses (glucosinolates and anthocyanins) once actual caterpillars started to feed on

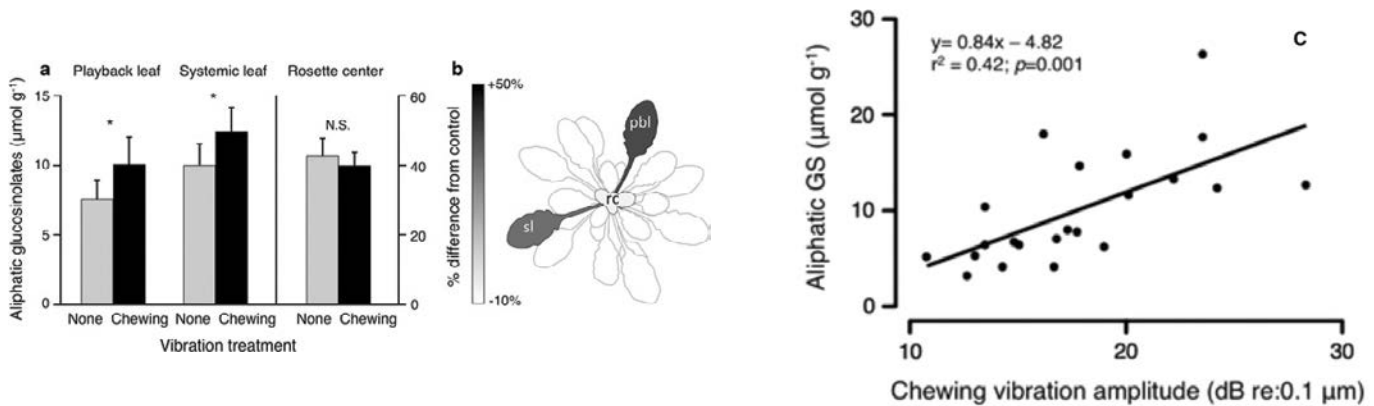


Figure 3. a: Playback of caterpillar feeding vibrations increased the induced response of *A. thaliana* to herbivore damage compared with no-vibration controls: * $P < 0.05$; error bars 95% confidence; $N = 44/\text{bar}$ (43 for rosette center); N.S., not significant. **b:** Gray scale map showing the increase in chemical response in the playback leaves (pbl) and same-age systemic leaves (sl), expressed as the percent change from the levels in control plants. **c:** Relationship between the amplitude of chewing vibration playbacks and the chemical defensive response ($N = 22$). GS, glucosinolates. Reproduced from Appel and Cocroft, 2014.

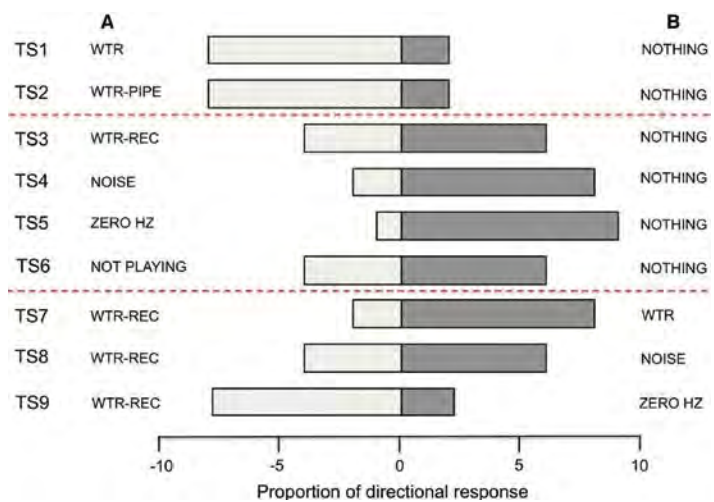
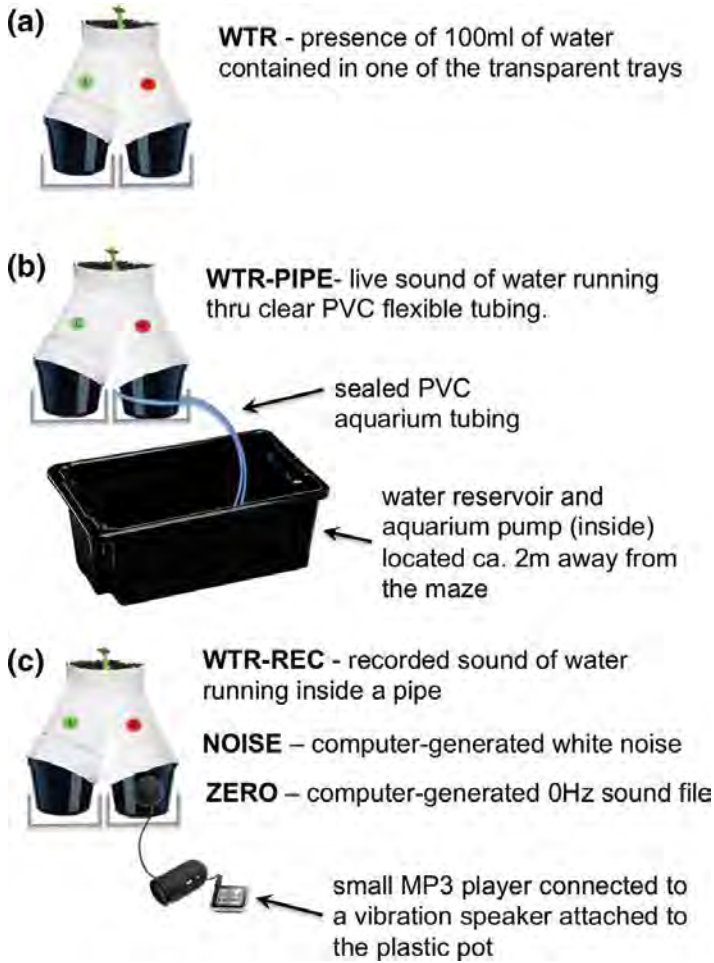
the leaves. In other words, sound had a “priming” effect on the chemical defenses of the plant. The caterpillar sounds were initially recorded with a laser Doppler vibrometer and then reproduced using piezoelectric actuators supported under a leaf, mimicking the duty cycle and source level of the original signals with as much fidelity as possible. Two plants received playback while an additional two had an actuator attached but no playback. Playbacks of wind and leafhopper insect calls (which occupy a similar spectral range as the caterpillars) were also conducted. Each test plant had two leaves removed and were tested for chemical defense expression; one leaf had the piezoelectric actuator attached, and the other (systemic) leaf was selected from the part of the rosette most distant from the activated leaf. **Figure 3** illustrates that the authors found that chemical defense concentrations rose 32% in the directly activated leaves and 24% in the more distant leaves and that increasing the amplitude of the playbacks corresponded with increasing concentrations of chemical response. Playbacks of the other two sounds yielded responses statistically indistinguishable from the control.

Monica Gagliano is another researcher who has consistently published work on potential plant responses to sound, with a particular focus on root growth in response to sound playbacks. Her work seems representative of modern playback experiments. After some initial work showing that bean sprout roots grow toward 200-Hz playback tones, Gagliano and her colleagues (2017) described how garden pea roots

responded differentially to accessible water, flowing (but inaccessible) water, and recorded sounds of flowing water. To demonstrate this, the authors gave growing plant roots an opportunity to grow into one of two plastic trays, one of which served as a control, and the other was exposed either to a PVC tube containing inaccessible moving water (while keeping the soil temperature constant) or to a speaker broadcasting back the circulating water sound (**Figure 4**). They found strong evidence that the presence of water circulating in a PVC pipe attracted root growth even though the water was not accessible and the temperatures remained the same (scenarios TS1 and TS2). Oddly enough, they found the presence of the embedded speaker and MP3 playback device seemed to repeal root growth regardless of whether and what type of sound was played (scenarios TS3-TS6). They then modified the experiment so that both plastic trays were outfitted with playback systems but with only one broadcasting flowing water sound (scenarios TS7-TS9). Only then did they note a preference in root growth toward the water playback compared with a speaker generating no signal (TS9), but the roots didn’t seem to be able to distinguish between flowing water noise and white noise (TS8). The authors speculate that magnets in the attached speaker might have influenced the response of the roots as well.

Both of these experiments illustrate the difficulties involved in measuring potential plant responses to sound. Isolating the effects of sound and vibration from other potential environmental cues (temperature, chemical release, physical

Figure 4. a-c: Experimental setup configurations showing treatment (red) and control (green) root cups. **A and B:** number of seedlings that directed their roots toward the treatment side (white bars) across all test scenarios (scenarios TS1 to TS9). Gray bars, seedlings that did not choose the treatment side; red dashed lines, distinct scenarios. See text for more details. Reprinted from Gagliano et al., 2017, with permission.



contact, magnetism) is difficult, as is accurately replicating the spectrum, amplitude, and temporal structure of the sound stimulus. There also remains the fundamental question as to whether plants are potentially responding to short-range mechanical vibration, near-field acoustic particle motion, or true acoustic sound, in the sense of a far-field airborne pressure perturbation (ten Cate, 2013).

Despite these challenges, a growth spurt of new results over the past two decades has stimulated a parallel theoretical debate in the literature about potential underlying mechanisms for sound reception and response: alterations in gene transcription, soluble protein content, or other cellular level effects such as changes in the plasma membrane protein structure of microfilament rearrangements (Hilker et al., 2016; Mishra et al., 2016). The state of the discussion at present seems reminiscent of the arguments about continental drift at the turn of the twentieth century; there was empirical evidence that continents had shifted their positions in the past, but no one could provide a theoretical explanation into how granite-based continents could plow across basaltic sea floors. It remains uncertain where the present debate will go, but it seems certain that improved low-cost acoustic playback equipment and better experimental technique have added new fertilizer to some old questions.

Taking Root in the Acoustical Society of America

Plant bioacoustics covers many different fields of expertise and many different topics, but a consistent feature about most of this research is that the advent of modern signal processing has opened up many opportunities for field biologists to explore the topic. Another consistent feature is that very little of it has been presented at ASA conferences or published in *The Journal of the Acoustical Society of America*. Instead, the work has generally been presented in biological or agricultural journals. One wonders whether the current organization of the technical committees of the Society makes it difficult for plant bioacoustic research to find a natural venue, and if so, whether the society may be missing an opportunity to branch out into a new frontier of bioacoustics.

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BioSketch



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