

Invited Commentary

Green symphonies or wind in the willows? Testing acoustic communication in plants

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Acoustic communication in plants lays an enticing vista of possibilities before us: new ways to test signalling hypotheses, exciting trophic interactions awaiting discovery, and unfamiliar mechanisms of signal production. But is this enthusiasm warranted? The review by [Gagliano \(2012\)](#) in this issue highlights some of the considerable hurdles to demonstrating acoustic communication in plants. Part of the excitement of plant communication is that the behavioral ecology community has a new opportunity to employ a rigorous research approach rooted in Tinbergen's ethological tradition ([Tinbergen 1963](#)). We propose that this approach needs to be identified clearly. To convincingly demonstrate that plant *communication* occurs as it is defined in the behavioral ecology literature, studies must show that 1) plants produce and respond to sound, 2) both traits provide an adaptive benefit, and 3) they have been historically selected for their communicative functions ([Williams 1966](#); [West-Eberhard 1992](#); [Autumn et al. 2002](#)).

PRODUCING AND RESPONDING TO SOUND

The first step is to seek evidence of plant responses to signals produced by other plants. [Gagliano \(2012\)](#) suggests several examples, but we are sceptical about how much support these provide. For instance, a study about acoustic gene regulation showed that rice plants alter their gene expression in response to classical music by Beethoven and others ([Jeong et al. 2008](#)). Admittedly, that study did not specifically aim to test plant responses to plant sounds, and [Jeong et al. \(2008\)](#) also found responses to single frequency signals between 50 and 250 Hz played back at 65–70 dB, which overlaps the frequency range of plant cavitation processes. However, rice plants do not produce classical symphonies, and it is uncertain whether they produce any sound whatsoever at intensities reaching 65–70 dB at a location where other plants could receive them. In this example, the response of rice plants to airborne sound is of limited value in the quest to establish whether plants communicate. We suggest that a different form of acoustic signal—substrate-borne vibrations—is a more plausible modality for plant communication. Substrate-borne vibrations can travel as much as several meters given the continuity of plant tissue ([Cocroft and Rodriguez 2005](#); [Hill 2008](#)) and can be produced at amplitudes necessary to signal to neighbors. Playback experiments using plant sounds recorded under realistic conditions would minimally establish the potential for plant communication. Such evidence could be gathered by obtaining recordings of stimuli that might be potential signals and presenting them to test plants at realistic intensities and rates. The key here is that the playback stimuli

should be both necessary and sufficient to induce a response in the test plants (cf. [Greenfield 2002](#)). The response should be induced by the playback alone, in the absence of any other environmental conditions that might normally be associated with production of the stimuli.

FITNESS BENEFITS OF PRODUCING AND RECEIVING ACOUSTIC SIGNALS

Bona fide communication in plants also demands mutual benefits, as [Gagliano \(2012\)](#) rightly points out, and demonstrating these is the second step of our proposed approach. [Gagliano \(2012\)](#) suggests that in the context of drought stress signallers might benefit by reducing the attractiveness of a patch to foraging herbivores, thereby decreasing their own predation risk. However, the benefits of acoustic signals are hard to envision owing to the fact that all plants within potential range of these signals are likely to be experiencing the same drought conditions. We also quibble with the characterization of acoustic signals as energetically inexpensive compared with other modalities such as chemical or visual signals. For example, if communication involves the collapse of specialized vascular tissues or physiologically suboptimal chloroplast movements, there may be considerable costs associated. One of the fundamental characteristics of acoustic signals in animals is that they attract unwanted attention from predators, a pattern repeated in singing insects, anurans, and other taxa ([Greenfield 2002](#)). We expect similar costs should apply to plants, decreasing the likelihood that the benefits of soliciting a response using an acoustic signal outweigh the potential costs of producing it.

SELECTION FOR COMMUNICATIVE FUNCTIONS

Establishing that a particular plant structure is specialized to produce a signal would provide definitive evidence that plant sound production is a trait that has been elaborated by selection. For example, there might be vascular tissues that are specialized to signal the risk of drought and collapse with less scarcity of water than most others. Or there might be mesophyll cells (or perhaps entire leaves?) that are specialized to signal a certain decrease or increase in light levels and that mobilize chloroplasts with less than the change in irradiance levels associated with adaptive physiological responses involving normal, homeostatically adaptive chloroplast mobilization (e.g., [Wada et al. 2003](#); [Tsuboi and Wada 2011](#); [Königer and Bollinger 2012](#)). Identifying such specialized structures could lead to studies examining how their development differs from nonspecialized structures, plus comparative analyses to test their phylogenetic origins as derived characters.

[Gagliano \(2012\)](#) has brought an extremely interesting idea to light and we credit her with noting several of the challenges highlighted above. However, going straight for the jugular of demonstrating plant communication is a conceptually demanding endeavor that we argue should be dissected into discrete steps in the order outlined above. Studying the use and potential production of sounds by plants provides a terrific opportunity to employ Tinbergen's

traditional ethological approach. We hope that future research will enlighten us as to whether plants do, indeed, trade acoustic signals for the purposes of communication, or whether plant sounds are like wind whistling through the branches of a willow: noticeable to us, but inconsequential to the plants.

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