Towards understanding plant bioacoustics

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Little is known about plant bioacoustics. Here, we present a rationale as to why the perception of sound and vibrations is likely to have also evolved in plants. We then explain how current evidence contributes to the view that plants may indeed benefit from mechanosensory mechanisms thus far unsuspected.

Plants vibrate at the rhythm of an evolutionary common sense

Many biological organisms use sound waves or vibrations for orientation or communication. Interestingly, apart from chemical signaling, much of animal communication depends on propagating waves, such as light, acoustic, electromagnetic waves. Evolutionarily, the reception and processing of the energy embedded in such waves is advantageous, as it allows for the gain of information about the environment, close by or distant. In effect, to perceive sound and/or mechanical vibrations, diverse organisms have evolved a diversity of sensory organs with adapted morphological structures and functions, and have tailored their sensory responses befittingly with the diverse sources, shapes and media through which vibrations propagate. For example, humans and most terrestrial mammals have evolved external auditory structures, the pinna, to collect airborne vibrations and transmit them to the eardrum, the first coupling stage of transformation of acoustical energy into mechanical energy. Yet, most auditory animals lack such external morphology, and many also have no eardrums. Birds and frogs have no outer ears, but their hearing can be more acute than ours. Many auditory insects also lack outer ears but still present eardrums that can be found at various locations on the body, depending on the species [1]. In mosquitoes and fruit flies, hearing is mediated by a very different morphological specialisation, antennae oscillating in the sound field endowed with a mechanically ultrasensitive Johnston's organ at their base. Remarkably, snakes lack both outer ears and eardrums, yet their jawbones act as coupling elements to pick up ground-borne vibrations, and deliver acoustic information to a cochlea-like mechanosensory system [2]. As sound travels readily and far in a dense substrate like soil, the snake's direct coupling to the substrate is a point in case; it is very efficient and enables the capture of information from distant sound sources.

Hearing research has shown that very different morphological structures can be functionally adapted to perform the biophysical task of sensing sounds and/or vibrations [3]. In fact, the reception and transduction of vibrational energy do not require the conventional auditory pathways of tympanate animals; eardrums and cochlear structures are just one possible, admittedly sophisticated, solution, but by no means constitute an essential requirement for hearing. Finally, given that substrate vibrations are present at all times and places, it can be surmised that those organisms that inhabit subterranean environments (e.g. fossorial mammals) or are indeed rooted within the ground (e.g. plants) benefit from some form of perception of substrate vibrations. Further hypothesis-driven research is clearly required to identify the ultimate functions of such sensory modality. A key question naturally resides in the nature of the sounds, and their information content. An integrated analysis of plant bioacoustical, behavioural and physical ecology is likely to yield key information as to whether, why and how plants sense sound and vibration in their environments. Altogether, it would be surprising not to find organisms endowed with mechanisms adapted to sensing and transducing ground vibrations. Another outstanding challenge is thus to reveal the biophysical and physiological mechanisms supporting sensitivity to substrate-borne sounds and explore their phylogenetic diversity. Within this context, we propose that the time is ripe to investigate the capacity of plants to detect and use sounds, be they in the form of substrate vibrations or airborne sounds.

The biophysical benchmarks for hearing and mechanoreception

Hearing and mechanoreception pertain to the reception and transduction of nanoscale vibrations. Displaying a vast diversity of anatomical features and functions, auditory and mechanosensory organs all have in common an exquisite sensitivity to mechanical forces. In effect, mechanical displacement magnitudes in the order of nanometers (range 0.1 nm to 1 μm) have been measured to be sufficient to elicit adequate neural response in such sensors [4]. At detection threshold, the mechanical energy imparted to such sensory structures is vanishingly small, sometimes barely above thermal noise [4]. By way of example, the human voice in a normal conversation is at approximately 60 dB sound pressure level (SPL), and can elicit vibrations in biological structures, not only hearing organs, of approximately 10–50 nm. Conceivably, provided with adequate mechanical properties (stiffness, damping), a soft biological structure, in the form of a hair (microtrichae or trichome) could serve as a sound receiver and

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pick up vibrations from its environment. Noteworthy is the fact that in dense environments, such as water and soil, the coupling of such structures is more efficient than in air, obviating the need for complex mechanisms providing impedance matching.

The existing evidence: plants detect and react to different sounds

The proximate and ultimate mechanisms used by animals to sense their environment and communicate with each other have long been the subject of intense scientific interest. In plants, sensory and communication research exists, yet is not as advanced and recognised. Existing evidence is enticing and calls for further investigation on the proximate, mechanistic question of how plants acquire and respond to acoustic information and further, demands the examination of ultimate, functional questions as to why such information bears adaptive value. In plants, both emission and detection of sound may be adaptive, as preliminary investigations of both processes (in particular reception) suggest (Figure 1a and b). Whilst receptor mechanisms in plants are still to be identified, there is early, yet tantalising, evidence about plants' ability of detecting vibrations and exhibiting a frequency-selective sensitivity that generate behavioural modifications (Figure 1b and c). At both proximate and ultimate levels, sound production in plants is only rarely documented and still poorly understood. We are growing increasingly doubtful of the idea that *all* acoustic emissions by plants are the mere result of the abrupt release of tension in the water-transport system [5]. We anticipate that plant acoustic radiation is not simply an incidental mechanical by-product attributable to cavitation alone; recent evidence illustrates that the young roots of corn generate

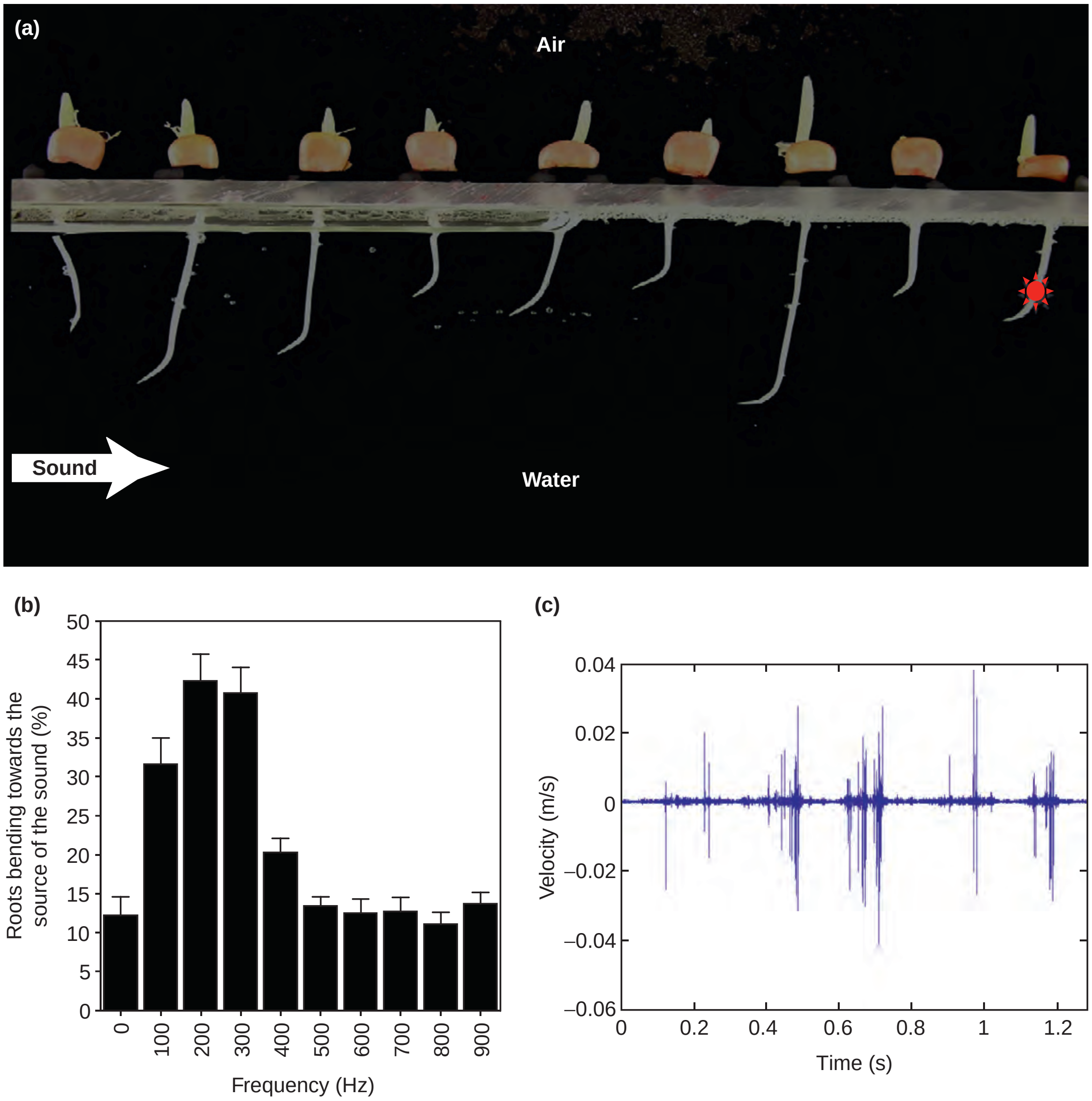

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Figure 1. Root bioacoustics. Behavioural response to incident sound, frequency selective response and acoustic emissions by roots in *Zea mays*. (**a**) Behavioural response of young roots to a continuous 220 Hz sound coming from left field (white arrow). Root tip clearly bend towards sound source. (**b**) Phonotropic assay assessing the response of young roots to water-borne vibrations (ca. 10 μm/s sound velocity level) at different frequencies. Best response is measured between 200 and 300 Hz. (**c**) Acoustic emissions of young roots measured optically with microscanning laser Doppler vibrometer. Vibrations were measured at the elongation zone of root tip (red star in panel **a**). Roots generate structured acoustic emissions in the form of loud (ca. 2 cm/s) and frequent clicks, which can also be measured at some distance into the fluid medium. (M. Pagano, PhD thesis, University of Firenze, in press).

structured, spike-like, acoustic emissions (Figure 1a). To date, the production mechanisms and adaptive value of such acoustic emissions remain elusive, yet in the past two decades several studies have pointed to the phenomenological importance of sound and vibrations in plant physiology (reviewed in [6]).

Because of the ease with which it transmits through the environment, sound can indeed offer a particularly effective transmission channel for short range signaling, possibly involved in modulating the swarm behavior of growing roots [7]. For long range signaling, other functions related to resource finding, intra- and/or extra-specific competition or cooperation, and growth orientation and coordination within the substrate can be envisaged. Acoustic and vibrational energy has other distinct dynamic advantages; it enables rapid and temporally well-defined, transient signal structures and responses to stimuli. Sound generation is also energetically much cheaper, yet not costless, than the production of volatile allelochemical messengers commonly used by plants. We propose that the potential adaptive functions of sound in the life of plants have not been explored to their full potential, leaving serious gaps in our current understanding of the sensory and communicative complexity of these organisms.

The promises and merits of a multidisciplinary approach

A considerable body of evidence emerging from contemporary research in plant science is increasingly recognising plants as highly sensitive organisms that perceive, assess, interact and even facilitate each other's life by actively acquiring information from their environment [8,9]. Much of this research has arisen at the interface between scientific disciplines, such as ecology and chemistry. As a successful example of interdisciplinary partnership, chemical ecology has greatly advanced our understanding of plants by unveiling their strikingly 'talkative' nature and the eloquent diversity of their volatile vocabulary [10]. Similarly, we reckon that multidisciplinary research is required for an effective exploration of the functional, ecological and ultimately evolutionary significance of acoustic communication in the life of plants. Enticingly, further research drawing from acoustical ecology, auditory mechanics and plant physiology is expected to transform our understanding of these organisms and galvanise the emergence of novel concepts and perspectives on plant communication. Such investigations may also, more generally, offer the unique opportunity to identify generic mechanisms subtending information processing in plants. Phylogenetically ancient, mechanoreception is deemed to a ubiquitous sensory modality. As such, mechanoreception underpins the behavioural organisation of all living organisms and their relationship with their environment; we propose here that it is very likely that some form of sensitivity to sound and vibrations also plays an important role in the life of plants.

References

1 Hoy, R.R. and Robert, D. (1996) Tympanal hearing in insects. *Annu. Rev. Entomol.* 41, 433–450
2 Young, B.A. (2003) Snake bioacoustics: toward a richer understanding of the behavioural ecology of snakes. *Q. Rev. Biol.* 78, 303–325
3 Yack, J.E. (2004) The structure and function of auditory chordotonal organs in insects. *Microsc. Res. Tech.* 63, 315–337
4 Robert, D. and Göpfert, M.C. (2002) Novel schemes for hearing and acoustic orientation in insects. *Curr. Opin. Neurobiol.* 12, 715–720
5 Zweifel, R. and Zeugin, F. (2008) Ultrasonic acoustic emissions in drought-stressed trees – more than signals from cavitation? *New Phytol.* 179, 1070–1079
6 Telewski, F.W. (2006) A unified hypothesis of mechanoreception in plants. *Am. J. Bot.* 93, 1466–1476
7 Karban, R. (2008) Plant behavior and communication. *Ecol. Lett.* 11, 727–739
8 Baluška, F. (2009) *Plant–environment Interactions–Signaling and Communication in Plants*, Springer-Verlag
9 Heil, M. and Ton, J. (2008) Long-distance signalling in plant defence. *Trends Plant Sci.* 13, 264–272
10 Ciszak, M. *et al.* (2012) Swarming behavior in plant roots. *PLoS ONE* 1, e29759

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