BIBLIOGRAPHIC INFORMATION SYSTEM

Journal Full Title: Journal of Biomedical Research & Environmental Sciences

Journal NLM Abbreviation: J Biomed Res Environ Sci

Journal Website Link: <https://www.jelsciences.com>

Journal ISSN: 2766-2276

Category: Multidisciplinary

Subject Areas: Medicine Group, Biology Group, General, Environmental Sciences

Topics Summation: 128

Issue Regularity: Monthly

Review Process type: Double Blind

Time to Publication: 7-14 Days

Indexing catalog: [Visit here](#)

Publication fee catalog: [Visit here](#)

DOI: 10.37871 ([CrossRef](#))

Plagiarism detection software: [iThenticate](#)

Managing entity: USA

Language: English

Research work collecting capability: Worldwide

Organized by: [SciRes Literature LLC](#)

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REVIEW ARTICLE

Understanding Acoustic Communication in Plants

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ABSTRACT

Responses of plants to environmental signals have been studied for a long time. These responses are exhibited in the form of morphological and physiological adaptations, and relaying the signal to environment (including other plants) through volatile organic compounds and extrinsic chemicals as well as proteins. However these signals do not correspond to the consciousness in the plants. Recent research in this field has produced evidence of non-physical signals e.g. sound and (electro) magnetic field. Plants produce such signals as well as perceive and respond to these signals. There are many novel techniques that have been used in last three-four decades to understand such signals, mostly acoustic signals. This review summarizes the old knowledge as well as recent developments in the area of generation, perception, integration and processing of acoustic signals by the plants as a response to the environment as well as to communicate among themselves. If understood fully, technological interventions and manipulations of these signals can add an extra tool for crop improvement.

INTRODUCTION

Plants communicate through many types of signals such as volatile organic compounds, electrical signals, common mycorrhizal networks, allelopathy and competition, species recognition and sound etc. There is much evidence to support the notion that plants also possess some degree of consciousness. Consciousness and its relevance to the plants have been vehemently debated [1,2]. Margulis and Sagan [3] defined consciousness as an awareness (has knowledge) of the outside world. In simple words it is the ability of the organisms to possess or generate, comprehend, process and transmit the electrical/magnetic/sound signals. Plants are able to generate, transmit and perceive some signals e.g., volatile chemicals [4], sound waves, magnetic signal and touch (thigmo) signals. Acoustic signals are most important of these and have been studied the most.

Acoustic signals are present in animals of which bat is an obvious example. New-born rats with limited locomotor and thermoregulatory abilities depend on the heat provided by the mother and siblings in the nest. When a pup wanders away from the nest, it emits Ultrasonic waves (USVs; around 40–kHz); mother can hear these USVs and respond. Authors [5,6] suggested that USVs are not stress calls rather a by-product acoustic signals as a result of thermoregulation process.

Why communication through sound is important

It is an important topic that has been debated a lot. For plants a communication signal is must since they can alert their neighbor about the stress. Contrarily, it can be speculated that there is no benefit of getting these signals as plants cannot move away from the impending danger/enemy. However plants have other several defense mechanisms e.g. they can make themselves untasty or harmful to herbivores, form

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DOI: 10.37871/jbres1314

Submitted: 04 September 2021

Accepted: 20 September 2021

Published: 21 September 2021

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OPEN ACCESS

Keywords

- Acoustic signals
- Chewing vibrations
- Magnetic signal
- Plants consciousness
- Sound perception
- Sound waves

BIOLOGY GROUP

BIOLOGY

VOLUME: 2 ISSUE: 9

How to cite this article: Vijay Kumar D. Understanding Acoustic Communication in Plants. J Biomed Res Environ Sci. 2021 Sept 21; 2(9): 815-820. doi: 10.37871/jbres1314, Article ID: JBRES1314, Available at: <https://www.jelsciences.com/articles/jbres1314.pdf>

odorous/bad smelling compounds or can make mechanical changes in their tissues (in long terms) to make themselves unpalatable for predators. Thus, evolving sound signals are beneficial for plants. From energy-economy point of view also sound signal is advantageous for plants as compared to chemical signals. Moreover transmission of such signals is comparatively faster. Noticeably, venus fly trap plants have mechanism to detect the nutritional value of the insect before deciding to trap it and also to differentiate between wind or other stimulus and insect stimulus. These signals might be sound waves but how plants perceive these signals is not clear as no such sound perceiving mechanism have been discovered in plants.

In a series of experiments, Singh and colleagues [7,8] showed that plants exposed to music experienced accelerated growth. Authors also reported that the violin provided the most prominent effect. They also found that barefoot, traditional Indian dancing in the same room as the plants caused them to flower two weeks earlier than previously recorded.

How plant communication can be experimentally evaluated

An important question is how plants perceive sound signal. One possibility is that they might have specific proteins that would change their conformation/configuration in response to sound waves. This can be evaluated through pure candidate proteins whose conformational changes can be detected through CD, intrinsic and extrinsic fluorescence, EPR and NMR spectroscopy i.e. zero-in at certain target proteins, express and purify them and study changes in their conformation through various kinds of spectroscopy. Second mode could be modulation of protein interactions with proteins, DNA, lipids or other macromolecules that could also be studied through various biochemical and spectroscopic methods. Interactions with proteins could be detected by performing native PAGE analysis of proteins after sound treatment, so as to determine any interacting proteins, including those from a changed configuration of protein. Third possibility is to look for mutants which are defective in generating/perceiving acoustic signals.

There are many chemicals/molecules that are present in certain quantities in healthy plants e.g. sugars (glucose, fructose, galactose etc.) and there are those which are induced in stressed plants e.g. reactive oxygen species (H_2O_2 , superoxide, singlet oxygen, hydroxyl radical and hydroxyl ion), reactive nitrogen species, stress signaling molecules (e.g. jasmonic acid, salicylic acid), ascorbate, glutathione, carotenoids, flavanoids, tocopherols, phenolics and proteins. Alternation in these molecules in response to (prolonged) sound can be estimated to check their response [9,10]. Beside this, photosynthesis response to sound can be measured by IRGA (CO_2 fixation levels; although difficult to detect minor changes) and Pulse Amplitude Modulator (fluorescence based) instruments. In addition, low levels of

plant responses have been detected through transcriptomics [11-16,19]. Detection of supposedly minor changes in above-mentioned molecules is technically challenging. Nonetheless, recent progress in technology has made it possible. Khait, et al. [17] detected sound waves emission from plants by recording very low intensity sounds and subtracting background sounds through machine learning program.

Further proposition about plant signaling can be based on the assumption that there are some elements that we don't know or the present science doesn't have the capacity to detect or comprehend them. It is already known that plants secrete some volatiles that can attract/repel the insects/herbivours/predators. There are some gases that act as stress signals. Appel and Croft [18] showed that if the plant is exposed to larva munching sound, it secretes ethylene gas, a stress signal to beware other plants.

Plants equivalent acoustic signals in animals

Similar to acoustic signals produced by plants [9,13,14,17,19] animals should also produce acoustic signals from organs other than mouth. But it might be of lesser degree since animals have mouth to produce sound and communicate. Anything that vibrates produces acoustic signal e.g. movement of actin fibers over myosin fibers. It is highly probable that the stressed and unstressed plants or animals (e.g. brains) give different signals which can be perceived by human, animals and plants because vibrational activities of organisms are expected to be different in these two states. Such signals are expected to be not a part of our conscious feelings/mind but perceived and processed by subconscious. In human, it is probable that such signals are produced/perceived by different people to different extents and as a result different people may have varied opinions about their existence.

How plants emit and respond to sound

One type of acoustic emissions are the result of the abrupt release of tension in the xylem following cavitation. When there is a stress in xylem, air bubbles form, expand, explode and empty spaces are formed which lead to the production of acoustic signals [20,21]. Many authors have termed acoustic signals as indicator of cavitation, particularly in drought-stressed plants [22-25]. However others argued that these plant sounds are induced by a largely stable bubble system of the xylem conduits capable of transporting water in travelling peristaltic waves [26]. Nonetheless, recent evidence indicate generation of sounds in plants independently of dehydration and cavitation-related processes [17]. A very plausible evidence was proposed by Khait, et al. [17] who found that plants emitted remotely-detectable and informative airborne ultrasonic sounds of frequency ~20-100 kHz under drought stress or upon cutting that were different from control plants and could be perceived by animals. One more example of plants

responding to sound is dehiscence of anthers which rely on the buzz sound produced by a specific bee and not by other bee species or insects who are pollen thieves [9,27].

There are ultrasounds and infrasounds beyond the human audible sound frequencies. Of these, ultrasounds have the greatest effect on plants, specifically on seed germination [28,29]. Ultrasounds altered the viscosity of macromolecule solutions in seeds. Near ultrasound waves (1.4 kHz, 0.095 kdb) increased amylase activity, soluble sugar, and protein content in *Chrysanthemum* roots [30]. The treatment of *Chrysanthemum* callus with sound waves of 1.4 kHz increased auxin (indoleacetic acid) and decreased ABA hormone contents [31].

The response of plants to sound, specifically music, has been discussed since long back [32,33-39]. Singh and Ponniah [7,8] reported the stimulatory influence of music on a number of plant species. Contrarily, Klein and Edsall [32] reported no influence of classical to rock and roll music, on the growth of *Tagetes erecta* L. Growth and seed germination of a number of plants was found to be influenced by music and single frequency sound in both audible and ultrasound range [28,33-35]. Similarly, increased rate of seed germination upon subjecting to music was reported in okra (*Abelmoschus*) and zucchini (*Cucurbita*) [36].

Acoustic response have further been reported in model plant Arabidopsis. Arabidopsis roots bent towards the sound of 20-200 kHz frequency [40]. Pea roots used sound to locate underground flowing water [41]. In tomato (*Solanum lycopersicum*), treatment with 1 kHz sound waves delayed fruit ripening by regulating the expression of ethylene biosynthesis related genes [42-44]. Kim, et al. [43,44] reported an increase in the antioxidant content of sprout vegetables upon being subjected to sound waves by regulating the expression of genes related to flavonoid and vitamin C biosynthesis [43,44]. Sound wave treatment significantly promoted germination and growth in *Oryza* and *Cucumis sativus* seeds [36,45]. Ultrasonic vibration of 20-105 kHz, emitted by barked plants, were detected by Laschimke, et al. [26] by connecting a sensor to the stem.

The hypocotyl elongation of Arabidopsis seedlings is also enhanced by sound waves [46]. Additionally, sound waves increased Indole Acetic Acid (IAA) levels, decreased Absciscic Acid (ABA) levels in chrysanthemum, and induced Gibberellin (GA), IAA, Salicylic Acid (SA) and Jasmonic Acid (JA) production in Arabidopsis [11,47]. 24 h of insect feeding vibrations caused changes in levels of phytohormones and Volatile Organic Compounds (VOCs) produced by leaves of *Arabidopsis thaliana* [18]. Indole-3-butyric acid (IAA) and Jasmonic Acid, hormone whose levels are known to be induced by wounding and MeJA application, showed even larger response upon additional treatment with feeding vibrations. Feeding vibrations caused an increase in β -ionone and decrease in methyl salicylate [48]. Feeding by chewing insects induces chemical defenses in plants that

are regulated by the Jasmonic Acid (JA) pathway. Feeding by *Pieris rapae* caterpillars induced a 1.8-fold increase in YFP fluorescence of a JA biosynthesis reporter [49]. Pre-treatment with feeding vibrations increased expression of the reporter in response to low MeJA concentration i.e. 14 μ M which would normally express at 115 μ M MeJA, although feeding vibrations did not potentiate responses at higher MeJA concentrations [49]. Feeding sound was proposed to be perceived in Arabidopsis through trichomes [50]. Trichomes showed vibrational modes that were in frequency range of the sounds of feeding caterpillars [50].

Arabidopsis seeds exposed to sound waves had increased roots length and cell numbers in the root apical meristem [39]. Genes of plant hormones-biosynthesis involved in root development i.e. cytokinin and ethylene signaling were downregulated, while auxin signaling and biosynthesis genes were upregulated in Arabidopsis roots, exposed to sound waves ((100 and 100 $\pm$ 9k Hz) for 15 h per day for 3 days) [39]. Correspondingly, the concentrations of cytokinin and auxin were modified [39].

Sound waves also elicited changes at the molecular and physiological level, including the levels of polyamines and uptake of oxygen [51], regulation of antioxidant enzymes [52], synthesis of RNA and soluble proteins [30,53], and gene expression [13]. Jeong, et al. [13] investigated ability of sound to alter gene expression in rice plants. Using complex musical sounds and single frequencies, authors isolated several sound-induced genes e.g. rubisco small subunit, calreticulin and a DNA-J-like protein. Furthermore, they demonstrated frequency-specific regulation of expression of cytoplasmic fructose, 1, 6-bisphosphate aldolase gene. Kim, et al. [15] also detected altered gene expression upon sound treatment. Two micro RNAs were also altered in tomato in response to specific sound wavelengths [15].

Plant Acoustic Frequency Technology (PAFT) is a recent development in field to improve plant yield, quality and disease resistance. It uses acoustic frequency generator to produce signals that match the frequency of the plant generated sounds [54]. Meng, et al. [55] determined that plant chlorophyll content, photosynthesis, number of flowers, fruits, yield and growth parameters of strawberry (*Frageria ananassa*) were improved when subjected to PAFT. The maximal fluorescence (Fm), maximum photochemical efficiency of photosystem II (Fv/Fm), and non-photochemical quenching (NPQ) increased markedly under PAFT treatment for 35 days [55].

Stress response of plants is also modulated through sound waves. Rice plants exposed to 0.8-1.5 kHz sound till 1 h demonstrated increased water contents and stomatal conductance, resulting in increased tolerance to drought stress [56]. Sound also induced drought tolerance in Arabidopsis [16].

Sound waves were also reported to alter the plants

responses to diseases. In a study on grapevines, continuous music treatment increased their resistance to pathogens [57]. Further, several different genera, e.g., *Bacillus*, *Kocuria* and *Sphingomonas* that showed a host-beneficial or pathogen-antagonistic effect, increased in phyllosphere. Moreover, several taxa that could potentially produce volatile organic compounds and contribute to sensory characteristics of wines e.g. *Methylobacterium*, *Sphingomonas*, *Bacillus* and *Sporobolomyces roseus*, either increased or appeared in the phyllosphere of core music-exposed grapevine population [57]. Algae also respond to sound e.g. sound treatment increased the growth of *Chlorella* by 12–30% [58].

At the cellular level, sound altered Ca^{2+} signals, rearrangement of microfilaments, ROS production, increased expression of amylases, kinases, peroxidases and other ROS detoxifying enzymes, H^+ -ATPase/ K^+ and increased production of soluble sugars, polyamines and auxins [9,13,14,52].

Communication through non-physical sources other than sound

In plants, there might be sources of communication/signals other than sound. Gagliano, et al. [38] demonstrated that when chilli plants are germinated around a fennel plant blocking all known source of signals such as touch, chemical or light, chilli seeds could still sense the presence of fennel plants in their vicinity and enhance their germination, probably to outcompete fennel seedlings. They proposed sound or magnetic field for the observed effect.

Seeds of chickpea (*Cicer arietinum* L.) when exposed to static magnetic field enhanced the germination rate, speed of germination, seedling length and seedling dry weight [59]. Moreover seeds exposed to such treatment significantly increased seedling dry weight of one month old plants, grown in soil [59]. Similar effects have been observed in multiple plants [60–62].

CONCLUSIONS

Environment drastically regulates the growth and development of plants. Plants respond to almost all environmental cues. Sunlight, temperature, humidity, different gases in the air and soil, organic and inorganic minerals, metals, pollutants in air and soil, various microbes etc. are such environmental cues that are perceived and responded to by plants. Sound is also present in environment and therefore plants should perceive and respond to it. The plants have for long time an association with animals including human, therefore it is important for plants to understand the human or animal behavior and communicate it speedily among themselves to relay the danger signal. Sound and different kinds of radiations including magnetic radiations could be such signals. As more advanced technology is emerging and being utilized

to study such aspects, it is becoming clearer that plants use non-material signals such as acoustic and magnetic signals to communicate. Plants produce sounds through cavitation [23–25] and other mechanisms [17,19,26] and respond to such sounds by modulation of gene expression, cell wall, enzyme activities, ROS, hormonal and transporters level, and altered primary and secondary metabolites [9,13–14]. Future research should be focused on finding the supportive evidence for mechanisms of sound emission and perception (e.g. a protein conformational change in response to sound). A thorough understanding of such phenomenon will lead to their application and commercial utilization for enhancement of yield and quality traits of crops.

ACKNOWLEDGMENTS

Funding

This work was supported by the Dayalbagh Educational Institute (DEI) internal grant, to VKD.

Contributions

This work was prepared in all aspects by VKD.

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How to cite this article: Vijay Kumar D. Understanding Acoustic Communication in Plants. J Biomed Res Environ Sci. 2021 Sept 21; 2(9): 815-820. doi: 10.37871/jbres1314, Article ID: JBRES1314, Available at: <https://www.jelsciences.com/articles/jbres1314.pdf>