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REVIEW ARTICLE

Phytoacoustics - Plants can perceive ambient sound and respond

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Abstract Responses of plants to a number of environmental stimuli such as light, gravity, and touch have been well investigated. However, response of plants to the sound remained doubtful for a long time. A number of recent studies have confirmed that plants do respond to sound vibrations of different intensities and combinations. They respond to the chewing sound of specific herbivores, sound of the pollinators and sound vibrations produced by moving water. Evidences have also been reported to indicate the ability of stressed plants to emit airborne sound. These recent studies indicate that plants, although sedentary without nervous system, have evolved, just like animals, to communicate with their environment in an ecologically meaningful manner.

Key words: Herbivores, Moving water, Music, Pollinators, Sound vibrations.

Introduction

The goal of any organism is to grow and reproduce by making adaptations to the prevailing environment. Animals are able to perform these functions effectively through their nervous system that enables them to modulate physiological and biochemical activities to utilize favourable environmental conditions to their advantage and to protect themselves from unfavourable conditions. This year's Nobel Prize in medicine was awarded for the discovery of receptors for temperature and touch that gives us the ability to sense touch, heat and cold on which our survival depends. Plants, which are sedentary, have to modulate their physiological and biochemical systems without an apparent nervous system. Never the less they have been able to make suitable adjustments to the prevailing environment, and have been able to evolve and thrive to colonize almost every terrestrial habitats.

There were hardly any serious studies to find out the mechanisms of such responses and modulations until the middle of the 19th century. Some biologists starting with the middle of the 19th century, conducted a number of experiments to understand how plants perceive and respond to environmental factors such as light, gravity, temperature, touch and sound. Jagadish Chandra Bose, a distinguished Indian physicist, who carried out extensive studies on plants and became an equally distinguished plant physiologist, was probably the first to indicate that plants also can perceive and respond to external stimuli (see Tandon 2019). He invented very sensitive instruments for detecting minute responses by living organisms and recorded many such responses to a variety of external stimuli. His demonstration of an apparent power of feeling in plants, exemplified by the quivering of injured plants, highlighted the parallelism between plants and animals. He believed that plants could feel pleasure and pain. One of his books *The Nervous Mechanism of Plants* (Bose 1926), and another *The Secret Life of Plants* (Tomkins and Bird 1973) summarise many of Bose's findings in the field of plant physiology. Unfortunately his findings were so revolutionary at the time that they arose only contradictions, criticisms and disbelief. His studies did not lead to further researches to test his concepts for several decades.

Subsequent advances in later years in plant

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physiology resulted in general acceptance of some of his findings. Many details as to how plants perceive and respond to external stimuli such as gravity, touch and light became well established since the time of Darwin and now we know a lot about these aspects (Sopory 2019, Mishra and Bae 2019, Veits *et al*. 2019). However, most of the historical studies on the perception of sound by plants continued to raise scepticism and doubts. A number of studies carried out in recent years, however, have convincingly shown that plants do perceive and respond to sound vibrations in an ecologically appropriate manner. This article summarises these recent developments.

Plants do perceive and respond to sound vibrations

Humans and many other terrestrial animals such as birds, frogs and several insects produce and perceive sound through various devices. The audible sound perceptible to humans has frequencies ranging from 20 Hz (Hertz) to 20000 Hz. The frequencies below 20 Hz (infrasound) and above 20 kHz (ultrasound) are not perceivable to humans. Most of the studies so far on plants' responses to sound were confined to growth responses on exposure to prolonged artificial acoustic stimuli and considerable literature has accumulated on this aspect (Chowdhury *et al.* 2014, Hassanien *et al*. 2014, Mishra *et al.* 2016, Jung *et al.* 2018, Mishra and Bae 2019, Veitz *et al.* 2019, Allievi *et al.* 2021).

Music is a coherent and harmonious blend of different frequencies, vibrations and intensities; it has many forms, qualities and pitches. T.C. Singh from the Department of Botany, Annamalai University, did many experiments during 1950s and 1960s on the effects of Indian classical music on plants. He recorded 20% higher growth and 72% increase in biomass in several plants such as rice, peanut and tobacco exposed to music. The book Sound of Music and Plants by Retallack (1973), apart from summarising earlier studies on applying music to plants to improve their health and yield, has described her own studies conducted at Colorado Women's College in Denver. She reported, for example, that plants leaned towards the radio playing classical and jazz music while they grew away from rock music. The results of earlier studies on the effects of music on plants were not consistent and remained debatable probably due to their use of different styles of music without standard uniform strength and vibration levels, and lack of effective controls. However, subsequent studies, particularly in China and South Korea, using standard technology has yielded convincing results on the beneficial effects of Indian and Western classical music. It has been reported to promote seed germination, plant growth leading to an improvement in the yield of several crops such as rice, wheat, tomato, cucumber and sweet pepper, and to make plants more tolerant to drought, increase their resistance to pests and diseases, enhance their immune system and delay in fruit ripening (see Hassanien *et al.* 2014, Mishra *et al.* 2016, Ghosh *et al.* 2016, Lai and Wu 2020, Munasinghe *et al.* 2020). Plants of rose for example, were reported to produce maximum elongation of shoot and maximum number of flowers with widest diameter when they were exposed to Vedic chants for 1 h in the morning for 62 days (Chivukula and Rangaswamy 2014). There are also reports that hard-core vibrations such as rock music produce negative effects such as bending of plants away from the source of music, reduction in the number of leaves, the size of flowers and production of higher number and density of thorns (see Chivukula and Rangaswamy 2014). At cellular level also, sound vibrations have been reported to increase transcription of certain genes and levels of soluble sugars, proteins, polyamines, enzymes, and also affect microfilament rearrangements (see Mishra et al. 2016). Ghosh *et al.* (2017) identified many genes upregulated by sound vibrations in *Arabidopsis*; their results indicated that sound vibration is perceived as distinct from touch, and the majority of genes regulated by sound vibrations are expressed spatiotemporally in different temporal stages such as imbibed seeds, seedlings and leaves. Additional studies carried out on *Arabidopsis* exposing plants of different ages to sound vibrations ranging from 200 Hz to 3000 Hz have reported a number of responses such as up-regulation of defence and salicylic acid, changes in gene expression, proteomics, transcriptomic and hormonal levels (see Khait *et al.* 2019a).

Responses of plants to vibrations of moving water

Responses of plants to music or any artificial sound does not indicate if they can respond to sources of natural sound emanating from their surroundings. This is important if plants have to modulate their responses to the environment in an ecologically meaningful manner. Some recent studies have shown that plants do respond to some natural environmental sounds (Gagliano *et al.* 2012). Water is one of the vital resources for all terrestrial organisms. Plants frequently encounter water scarcity and have strategies to search for water sources and direct their roots towards water source, largely based on moisture gradient. Using hydroponic system, Gagliano *et al.* (2012) showed that roots of corn seedlings are able to detect sound vibrations and use them for orientation of roots. Subsequent studies of Gagliano *et al.* (2017) showed that roots of *Pisum sativum* were able to locate the water source by perceiving the vibrations produced by water moving inside the pipes even in the absence of moisture gradient. In the presence of both water and other sounds, roots preferentially used water over other vibrations. The overall results of their study indicated that acoustic gradients enable the roots to detect water source at a distance and moisture gradients enable them to reach water target more accurately.

Plants perceive and respond to chewing sound of herbivores

One of the most important sound that emanates from the surrounding environment of plants comes from the herbivores and pollinators which land on the vegetative and floral parts of the plants. It is now well established that plants can perceive herbivore attack by their touch, egg laying or feeding, and activate various defence responses such as release of toxins or some volatiles or other chemicals to kill herbivores or attract predators or parasitoids of the herbivores (see Hilker and Meiners 2010). However, it was not known whether the sound produced by the herbivore could be recognized by plants. In recent years there has been some progress in understanding the responses of plants to the sound made by insect herbivores and pollinators. Appel and Crocroft (2014) subjected *Arabidopsis thaliana* plants to the vibrations caused by the feeding of insect herbivore, *Pieris rapae*. Treatment of the plant with vibrations caused during feeding of the caterpillar elicited synthesis of higher levels of the defence molecules, glucosinolate and anthocyanin (estimated 24 and 48 h after the treatment) when compared to controls (untreated plants). In another experiment, plants were treated with mating song of a leafhopper which has a similar frequency spectrum to that of chewing, and wind; this treatment did not elicit the synthesis of defence molecules. Thus, plants not only can perceive and respond to herbivory attack in an ecologically meaningful way but can also distinguish chewing vibrations from other environmental vibrations.

Plants can respond rapidly to the sound of insect pollinators

Effects of music was largely growth phenomenon which was slow and the responses of *Arabidopsis* to the chewing sound of the herbivore was studied 24 h and 48 h after the treatment. These studies do not reveal on the rapidity of the responses of plants to sounds emanating from the environment. It was known for quite some time that in addition to the fragrance, the flowers or leaves of several bat-pollinated plants are able to reflect the echoes of the ultrasonic emissions produced by their pollinator bats; reflected echo-acoustic characteristics enable the bats to locate such flowers (Helversen *et al.* 2003, Simon *et al.* 2011). Recently Veits *et al.* (2019) have been able to show rapid responses of the flowers to the sound produced by the pollinator. They used evening primrose (*Oenothera drummondii*) pollinated by hawkmoths and bees, and exposed the flowers for 3 min to the recordings of the sounds produced by the pollinator bee as well as to the synthetic sound at similar and different frequencies to the sound of the pollinator. They measured the concentration of sugar in the nectar and vibrations of the petals 3 min after exposure. Flowers exposed to recordings of the pollinator bee wingbeats produced nectar with significantly higher (1.2 times) concentration of sugar compared to those exposed to the sound of high frequency or no sound (silence). The flowers exposed to artificial sound of bee-like frequencies also resulted in increased nectar sugar. They also analysed physical vibrations of the flower in response to pollinator sound by using vibrometer. The flowers vibrated mechanically in response to airborne sounds of a bee or a moth recordings as well as the hovering of a live bee. The vibration amplitudes significantly decreased upon removal of the petals indicating the possibility of the petals serving as auditory sensory organ. This rapid increase in sugar concentration in the nectary, apart from preventing nectar robbery, is likely to increase the pollination efficiency in terms of increased number of visits and duration of visits of the pollinators to the flowers. These studies have opened up a new field of perception and rapid response of plants to sound in general and pollinators in particular.

Can plants produce airborne sound?

The studies described above show that plants can perceive and respond to the sound emanating from the surroundings. There were a few earlier reports that plants exposed to drought stress form air bubbles in the xylem that explode causing vibrations (Laschimke *et al.* 2006, Chowdhury *et al.* 2014, Jung *et al.* 2018); these vibrations could be recorded by connecting the device directly to the xylem (De Roo *et al.* 2016). It was not known if these vibrations could be sensed at a distance from the plant. Thus it was not clear whether plants can produce airborne sound that can be heard and induce responses in the surrounding organisms. Recently strong evidences have emerged to indicate that stressed plants emit airborne sounds, similar to stressed animals, that can be recorded both in acoustic chambers and greenhouses, and could potentially be heard by other organisms (Khait *et al.* 2019b). Plants of tomato and tobacco were subjected to drought stress and stress induced by cutting of the stem, and the responses were compared to the untreated controls. Stressed plants emitted significantly more sounds in the acoustic chamber and in the greenhouse in the ultrasonic range (of about 20-100 kHz, too high for humans to hear but can be heard by ultrasonic sensitive animals such as moths and bats moving around the plants) than those of the controls. This is the first report on the ability of stressed plants to emit informative airborne sound which could potentially be detected by other organisms. The sound emitted by stressed plants could be detected from a distance of 3-5 m by many animals sensitive to ultrasound. Thus we may not consider plants to be silent anymore! This paper is published in bioRxiv preprint and probably may require additional data before it is published in a peer reviewed journal. Nevertheless these studies have opened up another dimension of phytoacoustics. Further studies on these lines may lead to monitoring of crop plants to different stresses which would enable precision mitigation leading to an increase in crop productivity.

Conclusions

Over the years considerable number of studies have shown that plants are more communicative with their environment than what we thought, and seem to perceive most of the mechanical stimuli that animals perceive. Now the scepticism associated with the perception of sound vibrations by plants has gone and the focus has shifted to understand the mechanism of perception and its practical application (Mishra and Bae 2019, Allievi *et al.* 2021). Even in the absence of nervous system, development of mechanisms to perceive and respond to multitude of stimuli prevailing in the environment is probably the key for the evolutionary success of plants. Of course, a lot more need to be understood on these responses to manipulate them effectively for human benefit. Recently claims have been made on the existence of primitive eusociality, so far restricted to animal kingdom, in an epiphytic fern, *Platycerium bifurcatum* (Burns *et al.* 2021), thus taking plants a step closer to animals in some respects.

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