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Render a sound dose: Effects of implementing acoustic frequencies on plants' physiology, biochemistry and genetic makeup

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Abstract

Like other environmental factors, Sound vibrations also reported to greatly influence the plants at physical, biochemical and gene level. Based on relevant literature, this manuscript discusses the influence of Sound vibration in stimulating various growth and developmental parameters in plants like seed germination, root elongation, photosynthesis, nutrient uptake, yield, post harvest shelf- life, and also highlights various researches carried out to support influence of acoustic frequencies in defense, metabolism, cell cycle, and production of secondary metabolites, hormones and enzymes. Application of wide range of sound frequencies, infrasonic to ultrasonic, could provide myriad possibilities in advancement of future agriculture; however, a more comprehensive knowledge on signalling and regulation mechanisms is required to exploit the full potential.

Keywords: Sound vibrations, acoustics cues, plant growth, plant biochemistry, proteins, hormones

Introduction

The plants are organism susceptible to diverse environmental threats, this cause the necessity of developing defenses, principally due to its sessile life (Haswell *et al.*, 2012) [48] and it is well accepted fact that, environmental factors can greatly influence the growth and development of plants, even the genetic character (Xiujuan *et al.*, 2003) [136]. Accordingly, plants have evolved themselves against environmental challenges with effective physiological and developmental modifications, for instance, thigmo-morphogenesis (Chehab *et al.*, 2009, 2012) [17, 18]. Interestingly, recent studies have indicated that sound vibration (SV) may act as a pressure wave, triggering thigmo-morphogenesis (reviewed by Mishra *et al.*, 2016) [91]. Moreover, the expression analysis of SV-regulated genes after touch treatment hints at the possibility that SV is perceived as a stimulus distinct from touch, even though there is close resemblance between these two stimuli at molecular level (Gosh *et al.*, 2017) [42].

Sound is an omnipresent feature (Theunissen and Elie, 2014) [114], defined as acoustic energy in the form of an oscillatory concussive pressure wave transmitted through gases, liquids and solids, and each sound is characterized by its wavelength (hertz, Hz), intensity (decibel, dB), speed, and direction (Shipman *et al.*, 2012) [108]. SV is considered to be a mechanical stimulus which has a great impact on the biological index of plants (Bochu *et al.*, 1998, 2001; Zhao *et al.*, 2000; Liu *et al.*, 2001; Yiyao *et al.*, 2002; Yi *et al.*, 2003a) [11, 8, 147, 85, 143, 140] and can create the thigmo-morphogenetic response in plants (Telewski, 2006) [112] that can either promote or suppress growth (Chowdhury *et al.*, 2014) [24]. The lowest frequency classification in the acoustic spectrum is infrasound that has a frequency range < 20 Hz, whereas ultrasound is defined as acoustic waves with frequencies >20 kHz, which has been widely used in medical practice. Ultrasound and infrasound can interact with biological tissues by thermal and mechanical processes (O'Brien, 2007; Whittingham *et al.*, 2007; Rokhina *et al.* 2009) [95, 132, 105]. Recent findings using cutting-edge technology, quality control for hertz and decibel levels, and the integration of big data have helped change the viewpoint about this new field as it has entered the realm of generally accepted science (Gagliano *et al.*, 2012; Chowdhury *et al.*, 2014; Mishra *et al.*, 2016) [39, 24, 91].

The perception and processing of vibrations in the form of sound waves are very advantageous from an ecological perspective that helps the plant to understand the environment around them (Morales *et al.*, 2010; Aggio *et al.*, 2012) [93, 1], therefore, it would be unjustified to exclude

plants from this exciting field of study (Mishra *et al.*, 2016)^[91]. A growing body of evidence emerging from biological studies on the response of plants to sound waves indicates that plants are highly sensitive organisms that generate and react (perceive and emit) to SV from their environment (Haswell *et al.*, 2012, Mishra *et al.*, 2016)^[48, 91]. Sound waves are source of mechanical stress that affect the growth and development of plants (Braam *et al.*, 1997)^[13]. Acoustic cues have been reported to give rise to various physiological and molecular changes in plants. (Ghosh *et al.*, 2017)^[42] and it has been suggested that plants use these signals to obtain information regarding their environments and thus, can alter and fine-tune their growth and development (Moreno *et al.*, 2017)^[94]. Retallack, DL in 1973,^[103] published a book titled, “The Sound of Music and Plant”, containing experiments with particular styles of music to plants and concluded that the best growth results were obtained when classical music was played. Previously, farmers and several scientists in Oriental countries applied “Green Music” (e.g. bird’s singing, cricket’s stridulating etc.) to plants in order to improve plant health and yield (Qin *et al.*, 2003)^[102]. Afterwards, the effects of music to improve crop yield and quality have been reported in tomato plants, barley and other vegetables (Hou and Mooneyham, 1999; Spillane, 1991; Xiao, 1990)^[52, 109, 134]. Moreover, rhythmic classical music and rhythmic music with dynamically changing lyrics reported to positively affected root elongation and mitotic division in onion root tips during germination. Creath and Schwartz, 2004^[29]; compared effects of music, noise, and healing energy using seed germination assay.

In nature plants are responsive towards natural sounds, for instance, specific frequencies of bee buzzing facilitate the pollination of flowers, since these sounds induce the release of pollen from plant anthers (De Luca and Vallejo-Marin, 2013)^[33]. In a similar way, bat dependent plants have adapted to the bats’ echo-location systems by providing acoustic reflectors to attract their animal partners (Sch€oner *et al.*, 2016)^[106]. Pre-treatment with vibrations caused by chewing sound of caterpillar has been noted to elicit plant defense against herbivore (Appel and Cocroft, 2014)^[4]. Recorded insect chewing sounds induce the production of defense chemicals (glucosinolate and anthocyanin) in *Arabidopsis*, (Appel and Cocroft, 2014)^[4] and elevated levels of polyamines in Chinese cabbage after the exposure of green music (Qin *et al.*, 2003)^[102]. Similarly, cuckoo, cricket and mixed insect songs reportedly showed a positive effect on the height of cowpeas during the seedling stage (Jun and Shiren, 2011)^[67]. Collectively, these findings suggest that plants respond to insects through sound, sometimes serving as warning signals or beneficial signals to the plant (Jung *et al.*, 2018)^[68]. This suggests an ecological and environmental relevance of plant-acoustic interaction.

Nowadays, it is in vogue to use SV in abiotic stress response, as an elicitor that improves growth conditions, energy metabolism, stress related gene expression, increase in secondary metabolites production and resistance to diseases (Collins and Foreman, 2001, Xiaocheng *et al.*, 2003, Hongbo *et al.*, 2008, Li *et al.*, 2008, Choi *et al.*, 2017)^[27, 135, 50, 79, 23]. Studies using highly sensitive sound receivers have surprisingly demonstrated that plants indeed make spontaneous sounds and even release sound emissions from their xylem (Borghetti *et al.*, 1989; Ritman and Milburn, 1990; Laschimke *et al.*, 2006)^[12, 104, 78]. It is suggested that a coherent bubble system of the xylem conduits operate as a force transmitting medium that transports water in travelling

waves (Laschimke *et al.*, 2006)^[78]; however, this contradicts the idea that the emitted low-dB range acoustic signals are caused only by cavitations (Mayr and Zublasing, 2010)^[87]. It is reported that when transpiration decreases, audible sound is released and transpiration increases, ultrasonic emission is released (Ritman and Milburn, 1990)^[104]. Moreover, SV are generated when the diameter of the xylem vessel decreases (H€oltt€a *et al.*, 2005)^[49].

Plant Acoustic Frequency Technology (PAFT), an emerging technique, aims to impose the plant with sound wave in special frequency which accords with plant meridian system to influence yield and decrease chemical fertilizer requirement (Meng *et al.*, 2012a)^[89]. Ghosh *et al.*, 2016^[42], proposed that like other external stimuli, SV can triggers cellular events like, ROS scavenging, altering metabolism and hormonal signalling. Phytohormonal analysis supports the fact by showing a relation between SV-mediated responses and plant hormonal levels. Currently, the application of SV is effective to obtain agricultural and biotechnological benefits, which permit the idea that it can be applied in agriculture precision systems (Fernandez-Jaramillo *et al.*, 2018)^[37]. Based on relevant literature, the following manuscript discusses the impact of SV at various levels of growth & development, and how it cause molecular and biochemical changes in the plants and role in triggering the immunity against biotic and abiotic stress. Further, benefits of acoustic cues in future agriculture are also mentioned:

Influence of SV on Plant Physiology (Growth and Development):

Audible sound wave technology has recently been applied to plants at various physiological growth stages, viz., seed germination, callus growth, endogenous hormones, mechanism of photosynthesis, and transcription of certain genes. (Zhang, 2012)^[146]. Moreover, results indicated that the acoustic frequency technology promotes plant growth, increases production and improves yield quality (Hassanien *et al.*, 2014)^[47].

Germination

Hageseth, in 1974^[45] investigated the effects of sound on the mathematical parameters (differential germination rate as a function of time) using various frequencies that described quantitatively the barley seed germination process. Bochu *et al.*, 2003^[10] reported an increase in the germination index when rice seeds were stimulated with a 400-Hz sound wave. Natural sounds of birds and echoes to okra and zucchini seeds showed a higher statistical significant effect on germination/sprouting (Creath and Schwartz, 2004)^[29]. Similarly, seeds of *Echinacea angustifolia* showed improved germination rate to sound stimulation at 100 dB and 1 kHz (Chuanren *et al.*, 2004)^[26]. Gagliano and Renton in 2013^[41], demonstrated how a Basil plant stimulates the germination of chilli seeds, even when all signal pathways between plants (chemical, touch and light) were blocked. Hassanien *et al.*, 2014^[47] reported an optimal sound stimulation for seed germination, at SPL of 100 dB and frequencies of 0.4-0.8 kHz every day for one hour. Likewise, ultrasonic treatments reported to have positive effects on the germination percentage of the aged tall fescue seeds and improved seedling growth in Russian wild rye (Liu *et al.*, 2016)^[83]. Using sound waves, pulsed to the right set of frequencies, for desirable plants could stimulate them to grow while undesirable plants (weeds) could be inhibited, thus affecting the plant at an energetic and sub molecular level (Hassanien *et al.*, 2014)^[47].

Growth and Yield

Sound treatments have been broadly applied to alter plant growth. Weinberger and Measures, 1979^[130] reported that sonication at 5 kHz and 92 dB led to stimulate tiller growth with an increase of plant dry weight and number of roots in Rideau winter wheat. Different types of sound have been demonstrated to increase the growth of mung bean, rice, cucumber and *Arabidopsis* seedlings (Takahashi *et al.*, 1992, Johnson *et al.*, 1998, Uchida and Yamamoto, 2014; Cai *et al.*, 2014)^[111, 66, 117, 14], and increased the root length in *Actinidia chinensis* (kiwi) and paddy rice (Bochu *et al.*, 2003, Yang *et al.*, 2004)^[10, 139]. Hou *et al.*, 1994^[55] reported 100 Hz frequency of an external sound showed positive impact on philodendron plant growth. Ultrasound has been successfully used to enhance the *Agrobacterium*-mediated transformation of several plants, such as *Glycine max*, *Vigna unguiculata*, *Triticum aestivum*, and *Zea mays* (Trick and Finer, 1997)^[116] and thus influencing growth and yield. Cotton plants, exposed to PAFT showed increased height, leaf width, number of boll-bearing branches and bolls, and weight of individual bolls (Hou *et al.*, 2010b)^[54]. Similarly, when exposed to PAFT generator, the yield of rice (in pots experiment and in the open field) increased in average by 25% and 5.7%, respectively and that of wheat increased in average by 17%, also improving the protein content of rice which was increased by 5.9 and 8.9%, respectively; starch, protein and fat content of wheat, increased by 6.3, 8.5 and 11.6%, respectively (Hou *et al.*, 2010a; Yu *et al.*, 2013)^[53, 144]. Sound waves from PAFT generator significantly increased the yield of sweet pepper, cucumber and tomato by 30.05, 37.1 and 13.2%, respectively. Furthermore, the yield of lettuce, spinach, cotton, rice, and wheat were increased by 19.6, 22.7, 11.4, 5.7, and 17.0%, respectively (Hassanien *et al.*, 2014)^[47]. Treatment of rice plants with PAFT resulted in the enhancement of both the grain yield and quality: while yield increased by 5.7%, protein content in the grains showed an increase of 8.9% (Hassanien *et al.*, 2014)^[47].

Some sounds seem to be capable of orienting root growth, for instance, the roots of *Zea mays* were reported to bend toward sound with a frequency of 100–300 Hz in the hydroponic system and *Pisum sativum* roots locate water by actively growing toward flowing water belowground (Gagliano *et al.*, 2012, 2017)^[39, 38], indicating that sound induces structural responses in plants. Effects of sound stimulation on the metabolism of *Chrysanthemum* roots illustrated that the growth of roots accelerated under certain sound stimulation (Jiayi *et al.*; 2003)^[64].

Nutrient uptake

Carlson D in 2013^[15] invented sonic bloom, which involves a unique combination of sound and foliar spray of seaweeds and found that in the frequency range of 3 to 5 kHz caused the stomata to open and increased the uptake of 'free' nutrients available in the atmosphere, including N and moisture. Sound waves were found to be efficient at getting the herbicide into the plant. Mature weeds can be sprayed with 50% less herbicide and biocide if also treated with sound waves. Therefore, sound waves can decrease the requirements for chemical fertilizer and pesticide.

The growth-enhancing effect of SVs could potentially reduce the usage of fertilizers by 25% (Hassanien *et al.*, 2014)^[47]. At 90 dB constant sound intensity level and 3 different frequency values as 600, 1240 and 1600 HZ, nutritional element (N, P, K, Mg, Ca, Fe and Zn) analysis were performed for *Nephrolepis Exaltata* and results indicated highest N, Mg and

Ca contents at 1240 Hz sound frequency; and the P and K contents as the highest at 600 Hz sound frequency. Uptake of, Fe and Zn, micro elements increased with the increase at the frequency (Özkurt *et al.*, 2016)^[97].

Photosynthesis

Continuous exposure to sound is thought to enhance plant growth by promoting CO₂ fixation (Uematsu *et al.*, 2012)^[2012]. SV could improve the activity of photosystem reaction centre, and enhance the electron transport and the photochemical efficiency of PS II (Meng *et al.*, 2012b)^[90]. Increased photosynthetic ability has been observed in strawberry and rice in response to sound treatment (Qi *et al.*, 2009; Zhou *et al.*, 2010 Meng *et al.*, 2012a; Jeong *et al.*, 2014)^[100, 152, 89, 58]. Moreover, absorption efficiency of light energy markedly increased by sound waves, which is resulted in more electron transport between original quinine receptors on the recipient side of PS II, more light energy used for photochemical reaction and finally less superfluous excitation energy (Aspinall and Paleg 1981; Meng *et al.* 2012b)^[5, 90]. Sound frequency with ≥ 0.8 kHz enhanced RWC, stomatal conductance and *Fv/Fm* ratio in drought stress environment in rice. H₂O₂ production in sound treated plant was declined compared to control. *Therma* CAM (Infra-red camera), showed that sound treated plant and leaf had less temperature compared to control (Jeong *et al.*, 2014)^[58].

Growth Hormones

High levels of endogenous IAA and low levels of ABA are favourable for the callus development and differentiation of mature callus. Introducing a sound frequency of 1.4 kHz and SPL of 95 dB, had significantly higher IAA levels and lower ABA than that of the control, implied that a specific gene expression system was associated with endogenous hormone, which was regulated by some signals generated by sound waves stimulation (Wang *et al.*, 2004)^[122]. Increased IAA levels and reduced ABA levels were also detected in *Chrysanthemum* when exposed to a 1.4 kHz sound stimulus (Bochu *et al.*, 2004)^[9]. The acoustic frequency significantly stimulated the producing of endogenous hormones, such as, IAA, GA and ZR and also increased its contents in many vegetables viz cucumber, tomato, muskmelon, cowpea, and eggplant (Huang and Jiang 2011; Zhu *et al.* 2011; Meng *et al.*, 2012b, Hassanien *et al.*, 2014; Wei *et al.*, 2012)^[57, 153, 90, 47, 129]. In *Arabidopsis*, treatment with 500 Hz induces the production of the growth-related hormones IAA and GA₃, and the defense related hormones, SA and JA (Ghosh *et al.*, 2016)^[43].

Defense

Sound waves can change the cell cycle (Wang *et al.*, 1998)^[123] and plant cells are suggested to have the ability to get gradually primed when exposed to certain environmental or chemical challenges (Conrath *et al.*, 2002)^[28]. Some stress-induced genes might be switched on under sound stimulation and the level of transcription increased (Wang *et al.*, 2003a, Shao *et al.*, 2008)^[126, 107]. Sound waves may also strengthen plant immune systems. For instance, daily repetitive or dose dependent touch treatment on *Arabidopsis* leaves increased resistance against *Botrytis cinerea* (Chehab *et al.*, 2012, Benikhlef *et al.*, 2013)^[18, 6]. Sound pre-treatment enhances plant immunity against subsequent pathogen attacks by activating the plant defense hormones SA & JA (Hassanien *et al.*, 2014; Ghosh *et al.*, 2016)^[47, 43]. The treatment of plants with specific sound frequencies increased the disease

resistance in pepper, cucumber, and tomato (Tian *et al.*, 2009)^[115]. The sound stimulation could enhance disease resistances and decrease requirements for chemical fertilizers and biocides (Zhang, 2012)^[146]. It has been proved that spider mite, aphids, gray mould, late blight and virus disease of tomatoes in the greenhouses decreased by 6, 8, 9, 11, and 8%, respectively, and the sheath blight of rice was reduced by 50%. (Hassanien *et al.*, 2014)^[47]. Plants can discriminate SVs emitted by the chewing of caterpillars from those caused by wind or other insects such as pollinators, suggesting that vibrations travel throughout the plant, stimulating other leaves (Appel and Cocroft, 2014)^[4]. The treated strawberries with the PAFT were grown stronger than the control group and had significantly higher resistance against disease and insects (Qi *et al.*, 2010)^[101].

Meta-analyses have demonstrated the occurrence of sound-mediated plant protection through the activation of the systemic immune response in crop plants such as pepper, cucumber, tomato, and strawberry (Hou *et al.*, 2009; Chowdhury *et al.*, 2014; Mishra *et al.*, 2016; Choi *et al.*, 2017)^[51, 24, 91, 23]. SVs have been found to exhibit increased immune responses against plant diseases and insect pests, for instance, the spread of sheath blight in rice has been found to be reduced by 50% as a result of SV treatment (Hassanien *et al.*, 2014)^[47]. The transcriptomic & qRT-PCR analysis was performed on *Botrytis cinerea* infected Arabidopsis plants pre-exposed to SV of 1 kHz with 100 dB. Results indicated up-regulation of several defense and SA-responsive and/or signalling genes. Based on these findings, Choi *et al.*, 2017^[23] proposed that SV treatment invigorates the plant defense system by regulating the SA-mediated priming effect, consequently promoting resistance in Arabidopsis against *B. cinerea*. Such priming also reported to be achieved by mechanical stimulation as well, and explain how previous exposure to mild stress enables the plant to respond effectively to new stress factors (Li *et al.*, 2011)^[81].

In addition to biotic stress responses, sound treatment increases plant tolerance to abiotic stresses such as drought. In a study under more natural conditions by Falik *et al.*, 2011^[36], it was shown that plants experiencing drought can generate a 'drought alarm', which successfully alerts neighbouring unstressed plants to close their stomata. It is thus likely that the drought signal (alarm) is generated by the roots and travelled through the soil for plant-to-plant communication. Rice exposed to 0.8–1.5 kHz sound waves for 1 hour showed increased tolerance to drought stress; with higher water contents and stomatal conductance than the control group (Jeong *et al.*, 2014)^[58].

Active oxygen species (AOS) have dual actions during plant stress responses (Dat *et al.*, 2000)^[32] and proposed as a central component of plant adaptation to both biotic and abiotic stresses (Kim *et al.*, 1998)^[72]. Up regulation of enzymes like SOD, CAT, POD, APX, that reduce the built up AOS, and protect plant cells from oxidative damage, determine the ability of plant to survive the stress. In *Chrysanthemum* seedlings it was observed that the activities of these protective enzymes increased in response to sound waves (Jia *et al.*, 2003b; Wang 2003c)^[61, 128]. The content of soluble proteins and the activity of SOD increased at 1 kHz and 100 dB. However, those indexes decreased when sound waves stimulation exceed 1 kHz and 100 dB (Yang *et al.*, 2003)^[138]. The effect of sound waves stress on *Dendrobium candidum* has shown that the activities of antioxidative enzymes were enhanced in different organs *viz* leaves, stems

and roots under initial treatment of sound wave stress (Li *et al.*, 2008)^[79].

Exposing plants to sound activates plant innate immunity and (more specifically) elicits representative SA and JA defense signaling pathways similar to those observed in response to different chemical triggers (Ghosh *et al.*, 2016)^[43]. Therefore, sound wave treatment can act as a new trigger (besides chemical triggers) to help plants in maintaining fitness against unfavourable conditions (Jung *et al.*, 2018)^[68].

Post harvest and shelf-life

SVs of 1 kHz were found to enhancing the postharvest shelf-life of tomato fruits by down-regulation of ethylene biosynthesis and expression of signalling-related genes and thus delaying ripening as compared to untreated tomato plants. (Kim *et al.*, 2015)^[74]. Furthermore, changes in surface colour and flesh firmness were delayed in the treated fruit.

Influence of SV on plant biochemistry

Cell Division

Ekici *et al.*, 2007^[35] reported a positive correlation between root elongation and mitotic index by giving sound waves treatment. SV test on yeast cells not only increased the growth rate of the yeast cells by 12% but also reduced biomass production by 14%. Such results imply that sound affects the cell level rather than the specific structure of the organism (Aggio *et al.*, 2012)^[1]. Moreover, the growth and propagation of *Chlorella pyrenoidosa* were significantly improved by sound waves at a sound frequency of 0.4 kHz (Jiang *et al.*, 2011, 2012)^[63, 62]. Microalgae *Haematococcus pluvialis* was cultivated with the addition of audible sound with titles "Blues for Elle" and "Far and Wide" and treatment "Blues for Elle" shows the highest growth rate of 0.03 per day (Christwardana and, Hadiyanto 2017)^[25].

Cell structure

Sound stimulation increased the cell wall and membrane fluidity, which facilitated cell division and growth (Keli *et al.*, 1999; Zhao *et al.*, 2002a)^[70, 149]. Wang *et al.*, 2002a^[120] studied the effects of cell wall calcium on the growth of *Chrysanthemum* callus under sound stimulation. Sound waves could greatly change the cell cycle of *Chrysanthemums*, accelerated the growth by decreasing the number of cells in G₀/G₁ and increasing in the S-phase (Wang *et al.* 2003b)^[127]. Sound stimulation also increased the fluidity of the physical state of lipids in plasmalemma and influenced the secondary structure of proteins in cell walls and plasmalemma (Yi *et al.*, 2003c)^[142] and thus aid membrane trafficking modulation (Apodaca, 2002)^[3] and metabolic activity acceleration (Yi *et al.*, 2003c)^[142]. Sound treatment triggers drought tolerance by changing the elasticity and flexibility of the cell wall, which affects the ability of plants to absorb water (Jeong *et al.*, 2014)^[58]. Wang *et al.*, in 2001^[125], reported that alternative stress of sound waves could change the cell membrane deformability.

However, the optimal sound frequency stimulation will change according to the exposure time and period of application. (Hassanien *et al.*, 2014)^[47]. It has been hypothesized that the cytoskeleton-plasma membrane-cell wall interface has an important role in SV perception (Gosh *et al.*, 2016)^[43]. In addition, membrane architecture changes in response to sound treatment, which may facilitate the movement of signalling components (Mishra *et al.*, 2016)^[91].

Proteins

A sound frequency of 5 kHz for 4 weeks enhanced the amount of alanine and glycine, whereas asparagine content was lower in the sonicated endosperm tissue of Rideau wheat grains compared to untreated controls (Measures and Weinberger, 1973) ^[88]. Moreover, the amount of tryptophan increased superficially with the ultrasound treatment (Cheng *et al.*, 2017) ^[21]. Sound at specific frequencies and intensities promoted the content of soluble proteins and sugars in the cytoplasm of *Dendranthema morifolium* callus (Zhao *et al.*, 2003) ^[148]. It is suggested that multi-frequency energy-gathered ultrasound multi-frequency energy-gathered ultrasound assisted alkaline could improve the degree of hydrolysis and microstructure of protein elution both were efficient methods to save the enzymolysis time compared with the control and both methods break up the microstructures (Yusof *et al.*, 2016, Li *et al.*, 2016) ^[145, 80].

Sound waves at different frequencies and strength have been shown to alter the secondary structure of cell wall proteins of tobacco by changing Amide I and Amide II bonds (Ziwei *et al.*, 1999) ^[154]. Ultrasound pretreatment can change the molecular structure of the proteins (proreolysis application in industries to produce peptides) and also accelerate the enzymolysis, as well as, substrate concentration, enzyme concentration, pH, and temperature. (Demirhan *et al.*, 2011, Li *et al.*, 2016) ^[34, 80]. The secondary structure of membrane protein is highly sensitive to the stimulation of sound waves and the change of the secondary structure of membrane protein (caused an increase in α -helix and a decrease in β -turn) may lead to the fluidity increase of the plasma membrane. The sound stimulation significantly decreased the phase transition temperature and the speed of cells growth (Sun and Xi, 1999; Zhao *et al.*, 2002c) ^[110, 151]. Pre-treatment of ultrasound technology decreased the particle height and surface roughness of glutelin, reduced the Young's modulus and stiffness of zein while increased its adhesion force (Jin *et al.*, 2016, Yang *et al.*, 2017) ^[65, 137] and enhanced the functionality of soy proteins by increasing the antioxidant activity of highly denatured soybean meal hydrolysate (Chen *et al.*, 2017) ^[19].

Enzymes

Ultrasound and heat synergistically increased the inactivation rate of watercress peroxidase, lemon and tomato juice pectin methylesterase (Cruz *et al.*, 2006, Kuldiloke *et al.*, 2007, Terefe *et al.*, 2009) ^[30, 76, 113]. In addition, the increase of amylase activity showed an advancement of sugar decomposition, hence the catabolism changed highly after the sound stimulation (Jia *et al.*, 2003a) ^[60]. In *Arabidopsis thaliana*, sound altered the expression of several enzymes involved in light reaction, Calvin cycle, glycolysis and TCA cycle, with majority of them being upregulated (Gosh *et al.*, 2016) ^[43]. Kapturowska *et al.*, 2012 ^[69] investigated lipolytic activity on the effect of ultrasound in the hydrolysis of p-nitrophenyl laurate in *Y. lipolytica* and evaluated low lipolytic activity due to denaturation as an effect of cavitation. Thermo-sonic inactivation of enzymes (like peroxidase) was recorded by Cheng *et al.*, 2013 ^[20].

Secondary metabolites

Hasan *et al.*, 2017 ^[46] reviewed the use of ultrasonication in culture cell and crop products for the increased production of plant secondary metabolites. It is possible to obtain some beneficial secondary metabolites by applying SV than by applying some others elicitors (Fernandez-Jaramillo *et al.*,

2018) ^[37]. Ultrasonic frequencies have been used to harvest secondary metabolites located in the vacuole from in vitro grown plant cells (Kilby and Hunter, 1990) ^[71]. Ginseng cells exposed to ultrasound increased their saponins by up to 75% (Lin *et al.*, 2001) ^[82]. Alfalfa (*Medicago sativa*) sprouts were exposed to a range of sound wave frequencies & results indicated that treated sprouts had a higher AsA (l-ascorbic acid) content than untreated sprout along with high the activity level of SOD (Kim *et al.*, 2017) ^[75].

Metabolism

The soluble sugar content, protein and amylase activity increased significantly by sound stimulation (Jia *et al.*, 2003a) ^[60] and in chrysanthemum, these parametrs showed a significant increase in response to SV, thus indicated that sound stimulation could enhance the metabolism of roots and the growth of *Chrysanthemum* (Yi, 2003b) ^[141]. The plants under SV treatment also showed an increase in polyamines, which has synergy with ROS to regulate Ca^{2+} - and K^{+} activity, this represent a cross-talk between ROS and PAs (Pottosin *et al.*, 2014; Qin *et al.*, 2003) ^[99, 102].

Ca^{2+} is influenced by sound stimulation. Upon SV stimulus, Ca^{2+} transients occur by an increasing of cytoplasmatic Ca^{2+} (Wang *et al.*, 2002, White and Broadley, 2003) ^[124, 131] and amplified plasma membrane Ca^{2+} -ATPase activity in *Aloe arborescens* (Liu *et al.*, 2006) ^[84]. Sound waves of 500 Hz have a significant impact in increasing the ATP content. Xiaocheng *et al.*, 2003 ^[135] suggested that there might be a regulatory mechanism in the plant that causes more sensibility to frequency than intensity. PM H^{+} -ATPase activity enhanced in sound waves treated *Chrysanthemum* calluses also, probably due to involvement of Calmodulin-dependent phosphorylation (Wang *et al.*, 2002b; Zhao *et al.*, 2002b) ^[121, 150]. In *mit*-transmembrane, sound stress increase the electric potential and thus providing higher latent energy or activating H^{+} -ATPase synthase for synthesizing more ATP (Bochu *et al.*, 2003) ^[7]. The H^{+} -ATPases create an important electrochemical gradient in the plasma of membrane which plays an important role in the response to stimulus such as SV (Mishra *et al.*, 2016) ^[91].

Influence of SV on plant at molecular level

Biotech crops provide key solutions for the challenge of global food security in the future due to population growth and climate change (Cho *et al.*, 2016) ^[22]. Recent studies using transcriptomic and proteomic analyses, showed that proper sound treatment has a positive effect on plant growth (Jung *et al.*, 2018) ^[68]. Stress-induced genes could switch on under sound stimulation (Hassanien *et al.*, 2014) ^[47]. According to the priming effect hypothesis, repeated external stimulation can be imprinted as molecular-memory in the form of epigenetic marks or protein synthesis within plant cells, which then prepare the plant for sturdy response against future biotic or abiotic stresses (Pastor *et al.*, 2013) ^[98]. Proteomics analysis indicated that proteins related to photosynthesis, stress and defense, nitrogen metabolism, and carbohydrate metabolism were highly expressed at 8 hour after 250 or 500 Hz sound exposure (Kwon *et al.*, 2012) ^[77]. The 1, 506-bp *ald* promoter was also found to be a sound-responsive promoter, indicating that specific frequencies of sound can regulate the expression of any gene fused with the *ald* promoter (Jeong *et al.*, 2008) ^[59]. Sound treatment increases expression of photosynthesis-related genes, such as those encoding fructose 1, 6-bisphosphate aldolase and the

rubisco small sub-unit, and may induce CO₂ fixation (Jeong *et al.*, 2008; Uematsu *et al.*, 2012) ^[59, 118].

Arabidopsis calmodulin like 38 (CML38) gene is upregulated in response to sound treatment in Arabidopsis leaves (Ghosh *et al.*, 2016) ^[43]. Moreover, sound wave stimulation accelerated the synthesis and total content of RNA (Xiujuan *et al.*, 2003; Hongbo *et al.*, 2008; Shao *et al.*, 2008) ^[136, 50, 107] but had no influence on DNA content. This result indicated that some stress-induced genes might be switched on under sound stimulation and the level of transcription increased (Xiujuan *et al.*, 2003) ^[136]. Expression of some genes, encoding mechano-sensitive ion channels (eg. MSL and MCA), which may recognize mechanical signals, was reported to differ between sound-exposed and touch-treated Arabidopsis plants (Ghosh *et al.*, 2017) ^[42].

Sound-treated tomato showed reduced ethylene production and delayed softening compared with the control. The expression of ethylene biosynthesis genes ACS2, ACS4, ACO1, E4, and E8 and ripening-related genes RIN, TAGL1, HB-1, NOR, and CNR was delayed in tomato treated with 1 kHz sound versus the control. Exposure to 1 kHz sound induces tomato fruit to remain firm for longer (Kim *et al.*, 2015) ^[74]. The expression of genes encoding transcription factors RIN and HB-1, which control the expression of ethylene-related genes, was also affected in tomato treated with sound stimuli (Kim *et al.*, 2016) ^[73].

The survival of drought-induced Arabidopsis plants to water deprivation was significantly higher in the sound treatment (24.8%) compared with plants kept in silence (13.3%). RNA-seq revealed significant up-regulation of 87 genes including 32 genes involved in abiotic stress responses, 31 genes involved in pathogen responses, 11 genes involved in oxidation-reduction processes, 5 involved in the regulation of transcription, 2 genes involved in protein phosphorylation/ dephosphorylation and 13 involved in JA or ethylene synthesis or responses. In addition, 2 genes involved in the responses to mechanical stimulus were also induced by sound; suggesting that touch and sound have at least partially common perception and signaling events (Lopez-Ribera and Vicent, 2017) ^[86]. Another study that scrutinizes the regulation of several genes (TCH4, LTP, MDAR3, GRX480, AIG1, WRKY51, DMR6, MYB29, LECTIN, RLP53, WRKY38, NUDX6, FMO1, PBS3, PME41, Pad4, EDS1, EDS5) in *Arabidopsis thaliana* treated with different single frequency SV is the presented by Choi *et al.*, 2017 ^[23].

Developmental stage-specific expression profiling suggested that the majority of the SV-Regulated Genes were expressed spatio-temporally in different developmental stages of *Arabidopsis*, especially in imbibed seed, seedlings and leaves (Ghosh *et al.*, 2017) ^[42]. The photosynthetic performance index in sound-treated Arabidopsis plants was lower compared with the control (Gosh *et al.*, 2017) ^[42] and the expression of different genes encoding for RuBisCO subunits was altered (Gosh *et al.*, 2016) ^[43]. On analysis of expression levels of AsA biosynthesis-related genes it was found that genes, including VTC1, VTC2, VTC4, GME, L-GalDH, GLDH, MDHAR, and DHAR1, displayed differential expression in response to sound wave treatment. Therefore, sound wave treatment may be a viable method for increasing the nutritional contents of sprouted vegetables (Kim *et al.*, 2017) ^[75].

Future prospects

1. Through abiotic mechanisms such as sound, the concentration of compounds of interest (secondary

metabolites) in plants can be increased, and defenses against diseases or pests can be generated and reinforced.

2. PAFT technology holds promising results in strengthen plant immune systems against plant diseases and insect pests (Hou *et al.*, 2010 a, b) ^[53, 54].
3. Drought-induced acoustic signals could be utilized for communicating with nearby neighbours in order to prepare them for the impending water scarcity (Gagliano, 2013) ^[40].
4. Application of SV may benefit Plant biotechnology and tissue culture. In plant tissue culture techniques, SVs have been suggested to increase organogenesis (da Silva and Dobranszki, 2014) ^[31].
5. Application of sound as elicitor presents advantages such as low cost, easy handling and maintenance compared to chemical elicitation methods. (Alassali and Cybulska, 2015; Ojekale *et al.*, 2016; Wink, 2015) ^[2, 96, 133].
6. Integrating acoustic technology with other domains of science like magnetic, optical, thermal and nuclear could lead to emergence of a single practical technology (Hassanien *et al.*, 2014) ^[47].
7. The technique of increasing natural plant transpiration through acoustic energy could be used to deliver biomolecules, agrochemicals, or future electronic materials at high spatiotemporal resolution to targeted areas in the plant; providing better interaction with plant physiology or to realize more sophisticated cyborg systems (Gomez *et al.*, 2017) ^[44].

Discussion

The previous studies have shown that sound waves at different SPL and frequencies, for a certain exposure time have affect on plants growth (Hassanien *et al.*, 2014) ^[47]. High frequency and intensity of sound can cause cell damage, but at a proper frequency and strength it can promote the growth of plant cells (Bochu *et al.*, 1998) ^[11]. It had been found that sound stimulation had an obvious effect on the growth and development of flower plants, but it is not reported on the differentially expressed genes and their expressing characteristics under sound stimulation (Hongbo *et al.*, 2008) ^[50]. Sound represents a potential new trigger for plant protection (Mishra *et al.*, 2016) ^[91]. Sound waves with specific frequencies and intensities can have positive effects on various plant biological indices including seed germination, root elongation, plant height, callus growth, cell cycling, signaling transduction systems, enzymatic and hormonal activities, and gene expression (Chowdhury *et al.*, 2014) ^[24].

The sound stimulation is also very efficient at getting the herbicides into the plant, and also decreases the requirements for chemical fertilizer and pesticide (15-25%) as well as decreasing the plants diseases and improving the plant immune systems (Hassanien *et al.*, 2014) ^[47]. The ultrasonic sounds can cause several biochemical changes in the plants, for example, Ultrasound denatures enzymes (Huang *et al.*, 2017) ^[56]. In addition to delaying fruit ripening, perhaps the quality and yields of post-harvest crops can be improved by sound treatment (Jung *et al.*, 2018) ^[68].

There appear many similarities in the sound and touch signalling pathways, and thus, the field of plant acoustics can benefit from the information available in signalling of thigmoresponses. Whole genome transcriptomic maps to identify all the genes specifically affected by the SV stimulus could well highlight the similarities and/or dissimilarities among the

acoustic and mechano-perceptions and help to decipher acoustic signaling in plants (Mishra *et al.*, 2016) ^[91].

The mechano-sensitive ion channels present in plasma membrane are highly modulated due to sound wave treatment that leads to differential Ca^{+2} signaling in plants and subsequent regulation of downstream signaling molecules (Mohanta, 2018) ^[92]. The analysis of pathogen related proteins and other biomarkers will help scientists optimize sounds to maximize sound-specific plant stress relief (van Loon, 1975) ^[119]. Controlled environment analysis must be focussed more precisely in future experiments, to avoid conflicting results or unfavourable effects on nearby flora & fauna (Hassanien *et al.*, 2014) ^[47]. We should be enthusiastic about this new emerging field of plant research that holds the promise to provide us with a new dimension to look at plant as a perceiving organism: much smarter and more sensitive to various environmental stimuli than we might think (Mishra *et al.*, 2016) ^[91].

Conclusion

To conclude, although the idea of plants communicating by sound is intriguing, there is still a long way to go (Cate, 2012) ^[16] before any final interpretation. The use of sound as a new plant trigger is in its infancy, but it has already shown great potential (Chowdhury *et al.*, 2014) ^[24]. It is important to elucidate the signalling pathways followed by plants in response to SV (Fernandez-Jaramillo *et al.*, 2018) ^[37] and molecular components involved in this pathway, for which ROS and sugar molecules are optimistic candidate. However, this new emerging technology seems easy to apply and promising, but more extensive research and finding are needed to overcome the contradictions. The field of acoustics in relation to plants can be used to meet out future food demands, of ever-growing population and can also avoid (at least decrease) chemical pollution due to usage of fertilizers and pesticides.

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