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SHORT COMMUNICATION

Drought tolerance induced by sound in Arabidopsis plants

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ABSTRACT

We examined the responses of sound-treated arabidopsis adult plants to water deprivation and the associated changes on gene expression. The survival of drought-induced plants was significantly higher in the sound treated plants (24,8%) compared with plants kept in silence (13,3%). RNA-seq revealed significant upregulation of 87 genes including 32 genes involved in abiotic stress responses, 31 involved in pathogen responses, 11 involved in oxidation-reduction processes, 5 involved in the regulation of transcription, 2 genes involved in protein phosphorylation/dephosphorylation and 13 involved in jasmonic acid 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.

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KEYWORDS
Bioacoustics; mechano-stimulus; touch; water stress; white noise

Sounds are mechanical waves of pressure that propagate through a transmission medium such as air. As a wave of pressure, the sound can be considered as a mechanical stimulus and it could have an influence on developmental and physiologic plant processes[35,17,29] Different types of sound have been demonstrated to increase the growth of mung bean, rice, cucumber and arabidopsis seedlings[34,20,5] increased the leaf area in young strawberry plants[31] and increased the root length in *Actinidia chinensis* and paddy rice[3,43] Some sounds seems to be capable of orienting root growth[13,12] and significantly increased the callus growth in *Dendranthema morifolium*[47] and *Chrysanthemum*.[40] There are also evidences that determinate sounds can influence the development of fruits, for example, delaying tomato fruit ripening,[22] has an influence in pollination, for example, in buzz-pollination the pollen from anthers is only released upon vibration at a particular frequency produced by bee buzz.[9] In a similar way, bat dependent plants have adapted to the bats' echolocation systems by providing acoustic reflectors to attract their animal partners.[33] Active acoustic signaling in plants has been proposed although it is still under discussion.[11]

Sound-induced changes in plants have also been observed at the physiologic level. Some sounds increased the photosynthetic state of strawberry plants[48,28] The photosynthetic performance index in sound-treated arabidopsis plants was lower compared with the control,[14] and the expression of different genes encoding for RuBisCO subunits was altered.[15] In arabidopsis, sound altered the expression of several enzymes involved in light reaction, Calvin cycle, glycolysis and TCA cycle, with majority of them being upregulated.[15] Sound alters the levels of some phytohormones: increased polyamine content in chinese cabbage and cucumber,[32] ethylene production was lower in the sound-treated tomatoes[22] and sound increased the level of indole acetic acid (IAA) and decreased the level of abscisic acid in *Chrysanthemum* calli.[4] In arabidopsis, sound induced changes in the levels of gibberelins, auxins, jasmonic and salicilic acids, but not in ABA.[15] Sound has also the ability to alter antioxidant activities[18,41,29,15] and to increase oxygen uptake,[32] thus appears that ROS signaling is a player for sound-mediated signaling. Sound also induces the accumulation of ATP[39,43,29] increases plasma membrane H^+-ATPase activity[38,44] induces a higher electrolyte leakage in arabidopsis,[14] alters the calcium flux and increases the concentration of intracellular Ca^{2+}[25,38,44,29] Additional observed changes in cell composition induced by sound are an increase in soluble sugars[19,45,47] changes in free amino acid contents[27] and the induction of lipid peroxidation.[24] Sound-induced changes in cell structure have also been observed. Sound altered the secondary structure of cell-wall proteins[49] and the plasma membrane fluidity and permeability[21,46,43,29]

Sound produced no significant increase of DNA content but enhanced the synthesis of RNA and soluble proteins in *Chrysanthemum*.[42] A significant increase in the expression of the rice genes coding for a fructose 1,6-bisphosphate aldolase (ald) and ribulose 1,5-bisphosphate carboxylase (Rubisco) small subunit (rbcS) was observed and the ald promoter was shown to respond to specific sound frequencies.[18] The expression level of several ethylene biosynthetic and ripening-regulated genes was influenced by sound in tomato fruits.[22] A recent microarray analysis in arabidopsis plants noted that several genes were differentially expressed after sound treatment[15] and some of them are also induced by mechanical stimulus.[14] Changes in protein accumulation were observed in response to sound.[15] Many respiratory genes/proteins were upregulated as well as amino

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Supplemental data for this article can be accessed on the publisher's website.

acid biosynthetic enzymes, enzymes related to protein metabolism, folding and degradation and genes involved in sulfur, nitrogen and carbohydrate metabolism.[15] The arabidopsis transcriptomic and proteomic analyses showed the induction/accumulation of several stress- and pathogen defense-related genes/proteins.[15] Induction of defense mechanism by sound was previously observed.[8] Sound enhanced the resistance of strawberry against diseases and insects,[31] vibration in arabidopsis leads to the accumulation of defense molecules[1] and sound increased their resistance against *Botrytis* infection.[7] The treatment of plants with specific sound frequencies increased the disease resistance in pepper, cucumber, and tomato.[36]

All these data suggest the existence of molecular mechanisms for sound perception and signal transduction in plants and sound seems to induce plants defense mechanisms against pathogens and against different abiotic stresses.

Our results were focused on determining possible effects of sound on drought resistance of *Arabidopsis thaliana* plants and on the possible induced changes in gene expression. A precise description of the methods used is presented in the Supplemental File 1.

To explore a possible effect of sound in plant drought resistance, 6-week-old Arabidopsis plants grown at 22°C with a 8/16-h light-dark photoperiod were treated with 10 h 100 dB of white noise at the middle of the dark period during one week. Control plants were kept in silence. Irrigation was stopped at the beginning of the sound treatment. After the 2 weeks of drought the plants were re-watered. The survival rates were calculated one week after re-watering (Supplemental File 2). Sound treated plants showed an increased drought tolerance and resulted in significantly higher survival rates compared with untreated plants (Fig. 1): 24,8% (± 3.81) of the sound-treated plants surveyed compared with 13,3% (± 3.16) of the plants kept silence. This difference is statistically significant and indicate that the white noise increases arabidopsis drought tolerance.

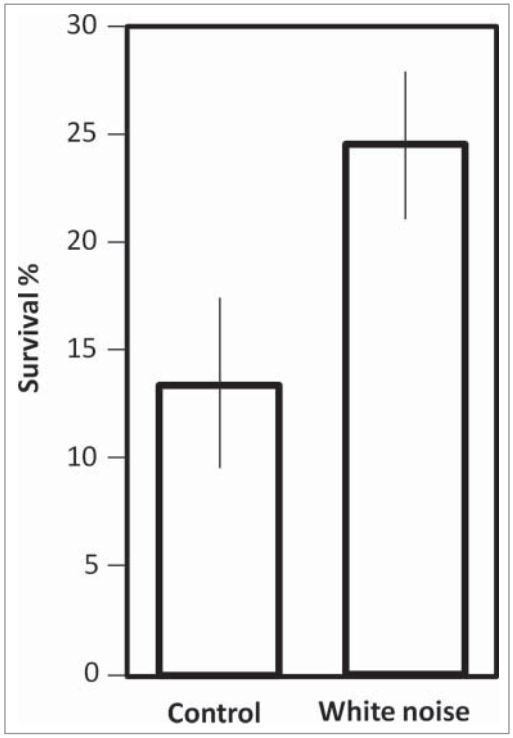

Figure 1. Increase in the drought resistance in arabidopsis plants exposed to white noise. The percentage of plant survival is indicated. Bars represent the standard errors.

The possible transcriptomic changes in arabidopsis upon exposure to sound were investigated through RNA-seq analysis. Six week old plants at the rosette stage were exposed during 10 h to 100 db white noise during the night and the samples were collected just at the end of the sound treatment. The samples corresponded to the eight youngest leaves of the rosette. The control samples were collected in the same moment with the only difference that the plants were not exposed to sound. Total RNA was extracted, cDNA libraries constructed and sequencing runs were performed in the Illumina HiSeq 2000 platform. A total of 3.65×10^8 reads were generated. Of the clean reads, 94.4% were uniquely mapped to the arabidopsis reference genome sequence. The normalized FPKM was used to quantify the gene expression level[37] to reveal differentially expressed genes. The expression of 89 genes was considered to be altered by sound (log2 fold change $> = 2$ and q-value < 0.05): 87 upregulated and 2 downregulated (Table 1). To validate RNA-seq results, RT-PCR was done to reveal the trend in the expression pattern of genes (Fig. 2). Expression of 6 genes was validated. In all the cases the RT-PCR results confirmed the patterns of expression obtained in the RNA-seq analysis.

A GO analysis was performed to determine the function of the identified differentially expressed genes (Supplemental Files 3 and 4). From the 87 upregulated genes, 44 (51%) are involved in responses to different types of stresses and the function of 22 is unknown. To confirm the enrichment in stress-related genes a GO enrichment analysis was performed (Table 2). Most of the 15 significantly overrepresented GO terms are related to stress, defense or response to stimulus.

Our results open new aspects of the discussion on the possible effects of sound on plants. Despite the growing data on different effects of sound in plants,[17,29] the detailed molecular events triggered by sound still remain mainly unknown. To get some more insight in this area, we performed an RNA-seq assay and we noted differential gene expression of many genes in arabidopsis rosette leaves and we found that sound treatment increases the tolerance to water deficit of the arabidopsis plants.

Different mechanisms have been proposed to explain sound effects on plants. For example, sound stimulation might cause leaves' stomata to open.[28] Another theory is that sounds induce in plants a similar response as touching (thigmomorphogenesis).[6] Like sound, touch is as an external mechanical force which interacts with the plant surface. Interestingly, described thigmomorphogenetic responses include resistance to other stresses. Transcriptomic studies had identified mechanoresponsive genes, including TOUCH genes (TCH) that mainly encode calmodulins or calmodulin-like proteins and xyloglucan endotransglycosylase/hydrolase (XTH),[6] genes encoding protein kinases,[30] transcription factors,[16] genes involved in jasmonic acid and ethylene synthesis[26,2] or genes involved in antioxidative responses.[10] A transcriptome analysis of touch-stimulated arabidopsis rosette leaves identified over 700 differentially expressed genes,[23] most of them upregulated. Up-regulated genes were specially enriched in calcium-binding proteins,

Table 1. List of the Significantly Induced Genes in arabidopsis leaves after white noise treatment (log2 fold change > = 2 and q-value < 0.05).

Gene_id	Gene	WN/CON	CON	WN	p-value	q-value
AT1G13607	Defensin-like	a	0,0	1,4	5,0e-05	0,00601
AT1G68825	Devil 5; Rotundifolia-like 15	a	0,0	0,4	2,0e-04	0,01862
AT2G31930	Unknown protein	a	0,0	0,9	5,0e-05	0,00601
AT4G01535	Unknown protein	a	0,0	1,4	5,0e-05	0,00601
AT5G38700	Cotton fiber protein	a	0,0	0,5	5,0e-05	0,00601
AT4G01360	BYPASS 3	41,6	0,2	7,9	5,0e-05	0,00601
AT4G30280	Xyloglucan endotransglucosylase /Hydrolase 18	26,5	0,5	12,0	5,0e-05	0,00601
AT1G35140	Exordium like 1; Phosphate-induced 1	25,1	0,5	12,0	5,0e-05	0,00601
AT5G52050	Detoxification efflux carrier 50	21,1	0,2	3,2	5,0e-05	0,00601
AT3G56790	RNA splicing factor-like	19,3	0,6	11,3	5,0e-05	0,00601
AT2G14247	Unknown protein	19,0	0,7	12,6	5,0e-05	0,00601
AT1G19210	DREB subfamily A-5 ERF/AP2 transcription factor	18,8	3,3	62,2	5,0e-05	0,00601
AT4G24580	ROP1 ENHANCER 1, Rho GTPase-activating protein	18,2	0,1	1,9	5,0e-05	0,00601
AT3G56970	Basic Helix-Loop-Helix 38; OBP3-Responsive Gene 3	15,6	0,7	11,0	5,0e-05	0,00601
AT1G50750	Aminotransferase-like mobile domain protein	14,3	0,2	3,1	5,0e-05	0,00601
AT2G17660	RPM1-interacting protein 4	12,6	0,9	10,7	5,0e-05	0,00601
AT3G02840	ARM repeat superfamily protein	11,5	11,1	126,7	5,0e-05	0,00601
AT3G44350	NAC domain containing protein 61	11,3	0,4	4,8	5,0e-05	0,00601
AT1G80840	WRKY DNA-binding protein 40	11,2	21,1	237,1	7,0e-04	0,04911
AT2G32130	Intracellular protein transporter putative (DUF641)	10,4	0,5	5,5	5,0e-05	0,00601
AT5G42380	Calmodulin like 37	10,4	4,5	47,2	5,0e-05	0,00601
AT3G23250	MYB domain protein 15	9,9	1,8	17,7	5,0e-05	0,00601
AT4G29780	Nuclease	9,9	17,8	175,2	5,0e-05	0,00601
AT3G01830	Calcium-binding EF-hand family protein	9,4	2,9	27,5	1,0e-04	0,01106
AT1G61340	F-BOX stress induced 1	8,9	4,6	40,7	5,0e-05	0,00601
AT5G22240	Ovate family protein 10	8,9	1,7	15,4	5,0e-05	0,00601
AT1G66090	Disease resistance protein TIR-NBS class	8,8	4,9	43,3	5,0e-05	0,00601
AT1G72520	Lipoxinegase 4	8,3	2,5	21,0	5,0e-05	0,00601
AT2G30020	MAPK phosphatase clade B of the PP2C-superfamily	7,9	33,0	259,2	5,0e-05	0,00601
AT5G57560	TOUCH 4; Xyloglucan endotransglucosylase/ hydrolase 22	7,5	20,4	153,5	5,0e-05	0,00601
AT2G35930	U-BOX 23; E3 ubiquitin ligase	7,2	7,8	55,6	5,0e-05	0,00601
AT5G45340	Cytochrome P450 family 707 Subfamily A Polypeptide 3	7,1	10,5	74,7	5,0e-05	0,00601
AT2G46400	WRKY DNA-binding protein 46	7,1	10,8	76,4	5,0e-05	0,00601
AT3G28340	Galactinol synthase 8; Galacturonosyl transferase-like 10	6,9	2,3	16,2	5,0e-05	0,00601
AT2G34600	Jasmonate-zim-domain protein 7; TIFY5B	6,9	1,2	8,6	5,0e-05	0,00601
AT3G46090	C2H2 and C2HC zinc fingers superfamily	6,8	1,6	10,9	5,0e-05	0,00601
AT1G22480	Cupredoxin superfamily protein	6,6	0,3	2,2	5,0e-05	0,00601
AT1G30135	Jasmonate-ZIM-domain protein 8	6,6	1,7	11,4	5,0e-05	0,00601
AT3G61190	BON Association protein 1	6,5	10,8	70,7	5,0e-05	0,00601
AT4G25490	C-Repeat/DRE Binding Factor 1; DRE Binding protein 1B	6,5	4,2	27,1	5,0e-05	0,00601
AT5G05390	Laccase 12	6,4	0,3	1,7	3,0e-04	0,02536
AT1G56660	MAEBL domain protein	6,4	7,2	46,1	5,0e-05	0,00601
AT3G52450	U-BOX 22 U-box domain E3 ubiquitin ligase	6,3	3,4	21,9	5,0e-05	0,00601
AT1G74930	DREB subfamily A-5 of ERF/AP2 transcription factor	6,1	43,4	263,4	5,0e-05	0,00601
AT1G17420	Lipoxynease 3	5,8	3,5	20,0	5,0e-05	0,00601
AT1G28480	Glutaredoxin GR480	5,7	5,1	29,2	5,0e-05	0,00601
AT1G76650	Calmodulin-Like 38	5,5	94,5	517,1	5,0e-05	0,00601
AT3G55980	Salt-inducible Zinc Finger 1	5,5	52,0	284,0	2,5e-04	0,02220
AT5G64870	SPFH/Band 7/PHB domain-containing membrane-associated	5,4	1,6	8,5	5,0e-05	0,00601

(*Continued on next page*)

Table 1. (Continued).

Gene_id	Gene	WN/CON	CON	WN	p-value	q-value
AT1G47400	Unknown protein	5,4	3,3	17,9	5,0e-05	0,00601
AT1G01560	MAP Kinase 11	5,4	4,1	22,3	5,0e-05	0,00601
AT5G35735	Auxin-responsive family protein	5,4	19,1	103,7	5,0e-05	0,00601
AT2G14610	Pathogenesis related 1	5,4	1,0	5,2	5,0e-05	0,00601
AT1G02400	Gibberellin 2-Oxidase 4	5,4	1,4	7,6	5,0e-05	0,00601
AT4G39670	Glycolipid transfer protein	5,3	5,4	28,6	5,0e-05	0,00601
AT5G47850	CRINKLY related 4	5,3	0,5	2,5	5,0e-05	0,00601
AT2G01180	Lipid phosphate phosphatase 1; Phosphatidic acid phosphatase 1	5,2	6,6	34,1	5,0e-05	0,00601
AT3G62260	Protein phosphatase 2C	5,1	11,6	59,2	5,0e-05	0,00601
AT1G74450	Unknown protein	5,1	24,6	124,1	5,0e-05	0,00601
AT5G66650	Calcium uniporter (DUF607)	5,0	4,2	21,0	5,0e-05	0,00601
AT2G14290	LL-diaminopimelate protein (DUF295)	5,0	0,3	1,3	5,5e-04	0,04080
AT1G18300	NUDIX Hydrolase homolog 4	4,7	92,6	438,8	5,0e-05	0,00601
AT4G11280	1-Aminocyclopropane-1-carboxylic acid synthase 6	4,7	32,3	152,8	1,0e-04	0,01106
AT4G25470	C-REPEAT/DRE binding factor 2; DRE/CRT-Binding protein 1C; Freezing tolerance QTL4	4,7	23,0	108,4	5,0e-05	0,00601
AT5G41750	Disease resistance protein (TIR-NBS-LRR class)	4,7	2,4	11,2	5,0e-05	0,00601
AT5G21960	DREB subfamily A-5 of ERF/AP2 transcription factor	4,7	7,7	36,0	5,0e-05	0,00601
AT1G66160	CYS MET PRO and GLY Protein 1	4,7	3,3	15,4	5,0e-05	0,00601
AT5G22545	Unknown protein	4,7	3,1	14,5	5,0e-05	0,00601
AT2G41640	Glycosyltransferase family 61	4,7	12,2	57,1	5,0e-05	0,00601
AT2G30040	Mitogen-activated protein kinase kinase kinase 14	4,6	9,0	41,8	5,0e-05	0,00601
AT5G64310	Arabinogalactan 1	4,6	20,7	95,7	5,0e-05	0,00601
AT2G23810	TETRASPANIN 8	4,6	39,9	182,8	5,0e-05	0,00601
AT1G47395	Unknown protein	4,5	8,6	38,7	5,0e-05	0,00601
AT1G60190	ATPUB19: U-BOX 19	4,5	14,4	64,8	5,0e-05	0,00601
AT1G72950	Disease resistance protein (TIR-NBS class)	4,5	2,0	8,9	5,0e-05	0,00601
AT2G40140	Salt-inducible Zinc Finger 2	4,5	26,5	118,3	1,0e-04	0,01106
AT1G02660	α/β-Hydrolases superfamily	4,5	1,2	5,2	5,0e-05	0,00601
AT4G24380	Dihydrofolate reductase	4,5	21,1	93,8	2,5e-04	0,02220
AT2G44840	Ethylene-responsive Element Binding Factor 13	4,4	6,9	30,5	5,0e-05	0,00601
AT5G05410	Dehydration-responsive element binding protein 2	4,4	1,1	4,8	1,5e-04	0,01528
AT1G17380	Jasmonate-ZIM-domain protein 5; TIFY11A	4,3	8,8	38,2	5,0e-05	0,00601
AT3G50930	Cytochrome BC1 Synhtesis; Outer Mitochondrial Membrane Protein	4,3	8,6	36,4	5,0e-05	0,00601
AT3G10930	IDA-LIKE7, IDL7	4,2	28,0	116,9	5,0e-05	0,00601
AT1G76600	Polymerase	4,2	20,2	84,3	5,0e-05	0,00601
AT2G39650	Cruciferin (DUF506)	4,1	6,4	26,1	5,0e-05	0,00601
AT3G46620	RING and DOMAIN of unknown function 1117 1	4,1	57,1	234,8	3,0e-04	0,02536
AT5G03210	DBP-Interacting-protein 2	4,1	30,2	122,3	5,0e-05	0,00601
ATCG01130	Translocon at the inner envelope membrane of chloroplasts 214	4,3[b]	0,7	0,2	5,0e-05	0,00601
AT4G03445	miR447A, targets several 2-phosphoglycerate kinase-related	c	1,1	0,0	6,0e-04	0,04335

[a]expression was only detected in the sound treated samples
[b]expression was higher in the control sample
[c]expression was only detected in the control samples

cell-wall proteins, disease resistance proteins, kinases and transcription factors.

Our RNA-seq results present similarities to what was observed after touch induction, for example, we also observed a predominant upregulation, and two genes directly involved in mechanical responses are among those upregulated genes: TCH4, encoding a xyloglucan endotransglucosylase/hydrolase, and ACS6, encoding the 1-aminocyclopropane-1-carboxylic acid synthase 6. White-noise upregulated genes include at least 32 genes involved in abiotic stress responses, 31 involved in pathogen responses, 11 involved in oxidation-reduction processes, 5 involved in transcription regulation, 2 genes involved in protein phosphorylation/dephosphorylation and 13 involved in jasmonic acid or ethylene synthesis or responses. Similar results were obtained in a microarray analysis based on single frequency treatments in Arabidiopsis.[15,12]

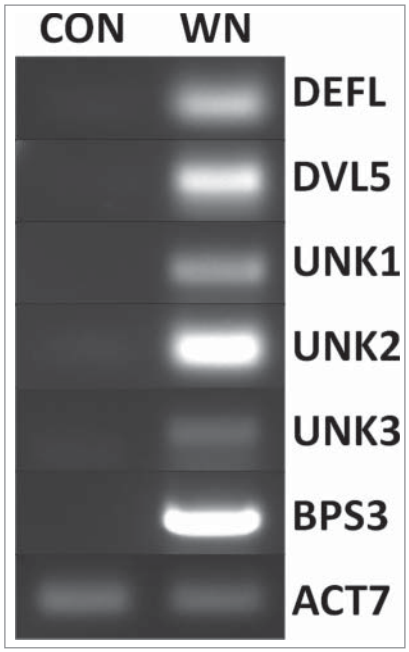

Figure 2. RT-PCR analysis of the expression profiles of 6 arabidopsis genes identified as differentially expressed by RNA-seq, all them significantly overexpressed in the sound treated plants (WN) respect to the controls (CON). Ethidium bromide stained 1.5% agarose gels showing RT-PCR products. The genes are (see Table 1): DEFL, At1g13607; DVL5, At1g68825; UNK1, At2g31930; UNK2, At4g01535; UNK3, At5g38700; BPS3, At4g01360. ACT7 corresponds to actin7 (At5g09810) and was used as control of non-induced gene. In each case, the size of the band shown is those expected.

Cell-walls play an important role in the perception of the mechanical stimulus.[35] We have identified at least four genes whose function is related to cell-walls: TCH4, laccase12, GOLS8 and XTH18. TCH4 encodes a cell-wall modifying enzyme that breaks the xyloglucan chains and make the cell-wall more elastic. The cell-wall interacts with the cell membrane, which, in turn, interacts with the cytoskeleton, which can modify the activity of ion channels, resulting in changes in the concentration of ions like calcium in the cytoplasm, which can activate several calcium binding proteins and kinases which can induce huge changes in the transcriptome and proteome, which eventually affect several vital processes, like growth, development and defense against pathogens or abiotic stresses. Supporting this hypothesis, two upregulated genes encode calcium related proteins: a calcium-binding EF-hand family protein and a calcium uniporter. Previous results also indicate that ROS signaling is another player for sound-mediated signaling.[32,18,41,29,15] We identified 11 upregulated genes involved in different aspects of oxidation-reduction processes. It thus appears that ROS signaling is an important player also for sound perception. Calcium, ROS and possibly hormonal changes may probably explain most of the effects of the sound response signaling previously observed as changes in the development and the induction of pathogen resistance, and also the induction of at least 32 genes involved in different aspects of abiotic stress, including 9 genes directly involved in water stress responses, and may explain our observed increase in water deficit tolerance.

We can conclude that sound has an impact on plants probably through a perception mechanism at least partially common to that of mechanical stimuli. Previous and our experiments demonstrate that plants can respond to sounds but each experiment has been performed using different parameters, so it is difficult to systematize the results. The conditions needed may depend on each species, the tissue and the phenomenon studied, or the frequencies, intensity or duration of the sound. Another interesting question is whether sound responses are relevant in natural conditions or just a side effect of mechanoperception. The acoustic responses of plants can offer insights into innovative practical applications such as reducing the negative effects of water deficit or a reduction in the use of pesticides. In

Table 2. GO ontology enrichment analysis showing significant over-represented functional categories in the leaves of sound treated arabidopsis plants compared with all genes.

Name of the annotation data category	Total[1]	Induced[2]	Expected[3]	Fold Enrichment[4]	P value[5]
Response to chitin	109	9	0,35	25,66	2.35E-07
Response to organonitrogen compound	154	10	0,50	20,18	2.08E-07
Response to nitrogen compound	228	11	0,73	15,00	5.15E-07
Response to wounding	182	8	0,59	13,66	3.31E-04
Response to jasmonic acid	172	7	0,55	12,65	3.40E-03
Response to acid chemical	886	21	2,85	7,37	1.37E-09
Response to oxygen-containing compound	1144	26	3,68	7,06	3.55E-12
	356	8	1,15	6,98	4.51E-02
Response to inorganic substance	690	13	2,22	5,86	7.38E-04
Response to organic substance	1466	22	4,72	4,66	2.25E-06
Defense response	1253	18	4,03	4,47	1.87E-04
Response to chemical	2084	28	6,70	4,18	8.04E-08
Response to stress	2639	31	8,49	3,65	1.50E-07
Response to abiotic stimulus	1491	17	4,80	3,54	1.05E-02
Response to stimulus	4612	40	14,84	2,70	8.66E-07

[1]Total number of genes in each annotation data category in *Arabidopsis thaliana*.
[2]The number of induced genes in each annotation data category.
[3]The number of genes you would expect in each annotation data category in *Arabidopsis thaliana* according to the total number of induced genes supposing a random distribution.
[4]Number of induced genes in each annotation data category divided by the expected number. If it is greater than 1, it indicates that the category is overrepresented.
[5]The p-value determined by the binomial statistic. This is the probability that the number of genes you observed in this category occurred by chance (randomly).

addition, the use of sound-induced promoters may have interesting biotechnological applications.

Disclosure of potential conflicts of interest

No potential conflicts of interests were disclosed

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Declaration of authorship

ILR performed the RNA extractions. CMV conceived and designed the experiments, analyzed the data and wrote the manuscript.

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