Title: The sounds of plants – Plants emit remotely-detectable ultrasounds that can reveal plant stress

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Abstract

Plants communicate with their environment in many ways, using colors and shapes and secreting chemicals. Yet, the possibility that plants emit airborne sounds that reveal their condition has not been investigated. Here, we develop a novel method for remotely detecting plant sound emission. We use it to demonstrate, to our knowledge for the first time, that plants emit sounds that can be recorded from a distance. We recorded ~65 dBSPL ultrasonic sounds at 10 cm distance from tomato and tobacco plants, suggesting that these sounds could be detected by many animals from up to several meters. We further train machine learning algorithms to identify the physiological condition of tomato and tobacco plants based solely on the emitted sounds. We successfully classified the plant's condition – dry, cut, or intact – based on its emitted sounds. Our results suggest that animals, and possibly even other plants, could use sounds emitted by plants to gain information about the plant's condition. More investigation on plant bioacoustics in general and on sound emission in plants in particular may open new avenues for understanding plants, and their interactions with the environment.

Introduction

Plants are constantly involved in communication (Karban 2008). When flowering plants are ready to breed, they attract their pollinators by releasing attractive fragrances and displaying bright colors (Raguso 2008, Renoult, Valido et al. 2014, Renoult, Blüthgen et al. 2015). When attacked by herbivores, plants can emit volatile organic compounds (VOCs) that attract their herbivores' predators, leading to an increase in the plant's survival and fitness (Takabayashi and Dicke 1996, Kessler and Baldwin 2001, Engelberth, Alborn et al. 2004). VOCs can also affect neighboring plants, resulting in increased resistance in these plants (Dolch and Tscharntke 2000, Heil and Karban 2010). Altogether, plants have been demonstrated to use visual, chemical and tactile communication (Karban 2008, Falik, Mordoch et al. 2011, Chamovitz 2012). Nevertheless, the ability of plants to emit airborne sounds – that could potentially be heard by other organisms – has not been explored (Chamovitz 2012, Gagliano, Mancuso et al. 2012, Hassanien, HOU et al. 2014).

Plants exposed to drought stress have been shown to experience cavitation – a process where air bubbles form and explode in the xylem, causing vibrations (Tyree and Sperry 1989, Cochard, Badel et al. 2013). Yet, these vibrations have always been recorded by connecting the recording device directly to the plant xylem (Cochard, Badel et al. 2013, De Roo, Vergeynst et al. 2016). Such contact-based recording does not reveal the extent to which these sound vibrations could be sensed at a distance from the plant, if at all (Bailey, Fowler-Finn et al. 2013, ten Cate 2013, De Roo, Vergeynst et al. 2016). Thus, the question of airborne sound emission by plants remains unanswered (Gagliano 2012, De Roo, Vergeynst et al. 2016, Jung, Kim et al. 2018).

Many animals, including herbivores and their predators, respond to sound (Spangler 1988, Miller and Surlykke 2001, Fullard, Dawson et al. 2003) . Recently, plants were also demonstrated to respond to sounds (Jeong, Shim et al. 2008, Hassanien, HOU et al. 2014, Ghosh, Mishra et al. 2016, Mishra, Ghosh et al. 2016), e.g. by changing gene expression of specific genes (Jeong, Shim et al. 2008, Ghosh, Mishra et al. 2016). If plants are capable of emitting informative airborne sounds, these sounds could have a rapid effect on nearby organisms, including both animals and plants. Even if the emission of the sounds is entirely involuntarily, and is merely a result of the plant's physiological condition, nearby organisms that are capable of hearing them could eavesdrop for their own benefit. Furthermore, some of these responses may be beneficial for the emitting plant, for example if the plant's sounds induce resistance to drought or disease (Kwon, Jeong et al. 2012, Jeong, Cho et al. 2014, Choi, Ghosh et al. 2017, López-Ribera and Vicient 2017) in neighboring plants – or even in other parts of the same plant. In such cases, plant sound emission would be favored by natural selection. Therefore, we hypothesize that plants emit informative airborne sounds, which may serve as potential signals to their environment. Here we show that plants indeed emit airborne sounds, which can be detected several meters away. Moreover, we show that the emitted sounds carry information about the state of the plant.

Results

To investigate plants' ability to emit airborne sound emissions, we constructed a reliable recording system, in which each plant was recorded simultaneously with two microphones (see Fig. 1 for illustration, and Methods for details). We recorded tomato (*Solanum lycopersicum*) and tobacco (*Nicotiana tabacum*) plants under different treatments, focusing on the ultrasonic sound range (15-250 kHz), where the background noise is weaker.

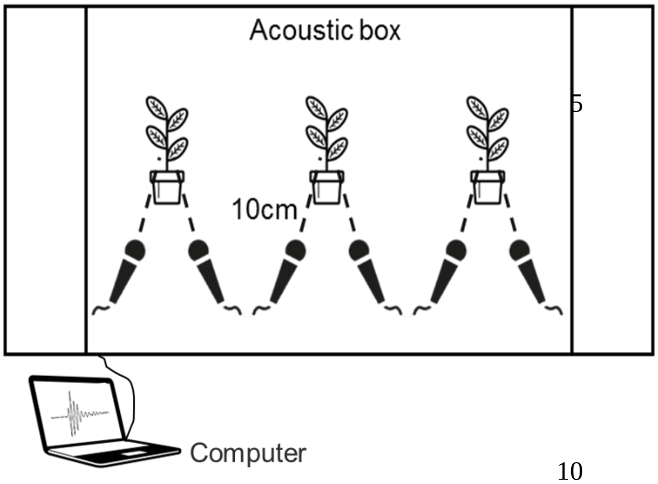

Figure 1. Experimental setup. In each recording, three plants are placed inside an acoustic box with two directional microphones oriented at each plant. Using two microphones helps eliminating false detections resulting from electrical noise clicks of the recording system and cross-plant interference. Two plant species were recorded: Solanum lycopersicum (tomato) and Nicotiana tabacum (tobacco).

We found that plants emit sounds, and that drought-stressed plants (see Methods) emit significantly more sounds than control plants (p<e-7, Wilcoxon test). The mean number of sounds emitted by drought-stressed plants during one hour was 35.4±6.1 and 11.0±1.4 sounds for tomato and tobacco, respectively (Fig. 2a). In contrast, the mean number of sounds emitted per hour by plants from all the well irrigated control groups was lower than 1 (Fig. 2a). Three controls were used: recording from the same plant before treatment (*self-control*), recording from an untreated same-species neighbor plant (*neighbor-control*, see Methods), and recording an empty pot without a plant (*Pot*). Our system did not record any sound in the *Pot* control (Fig. 2a).

How does a dry plant sound? Figs. 2b, c show examples of raw recorded time signals and their spectra as recorded from drought-stressed tomato and tobacco plants. The mean peak sound intensity recorded from drought-stressed tomato plants was 61.6±0.1 dBSPL at 10 cm, with a mean peak frequency of 49.6±0.4 kHz (frequency with maximal energy), and the mean intensity recorded from drought-stressed tobacco sounds was 65.6±0.4 dBSPL at 10.0 cm, with a mean frequency of 54.8±1.1 kHz.

Similarly to drought-stressed plants, cut plants (see Methods) also emitted significantly more sounds than control plants ($p<e-7$, Wilcoxon test). Cut tomato and tobacco plants emitted 25.2±3.2 and 15.2±2.6 sounds per hour, respectively (Fig. 2a), while the mean number of sounds emitted by control plants was lower than 1 (Fig. 2a). Figs. 2b, c show examples of recorded time signals and their spectra as recorded from cut tomato and tobacco plants. The mean peak intensity of the sounds emitted by cut tomato plants was 65.6±0.2 dBSPL at 10 cm distance with a mean peak frequency of 57.3±0.7 kHz (frequency with maximal energy), and the mean intensity of the sounds emitted by cut tobacco plants was 63.3±0.2 dBSPL at 10.0 cm distance with a mean frequency of 57.8±0.7 kHz. The distributions of sound peak intensity and the maximum energy frequency of cut and drought-stressed tomato and tobacco plants are shown at Fig. 3a. Spectrograms of raw recorded sounds from cut and drought-stressed tomato and tobacco plants are shown at Supporting Information Fig. S1.

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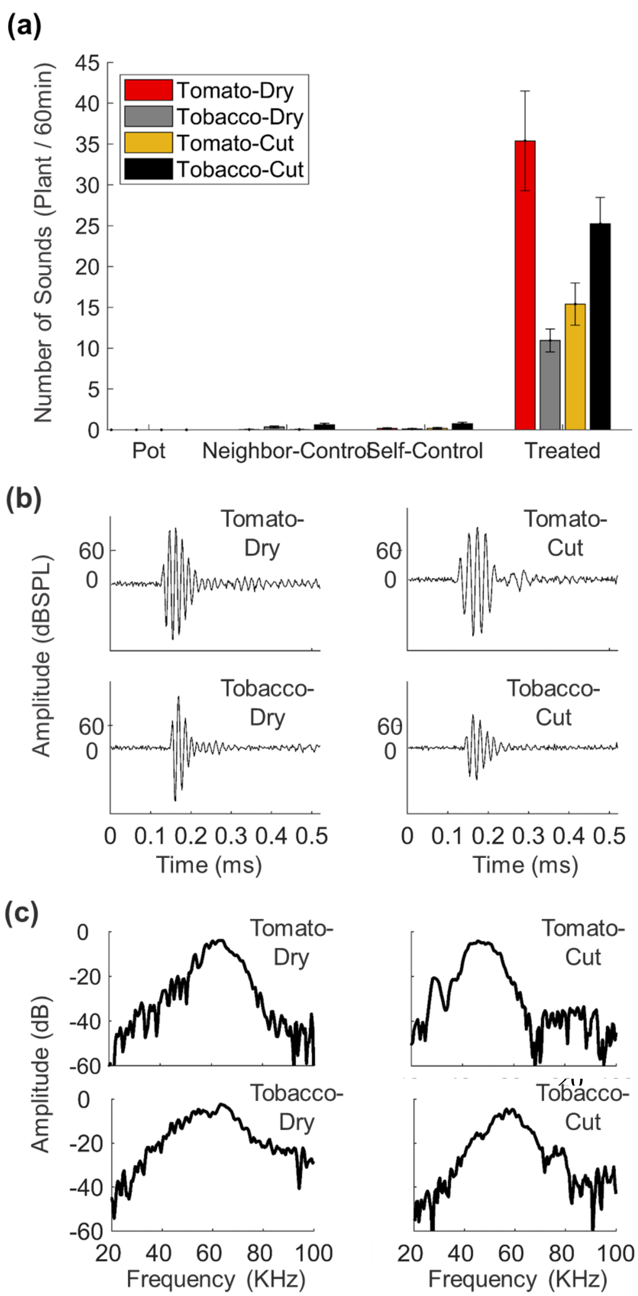

Figure 2. Plants emit remotely-detectable ultrasounds under stress. (a) Mean number of sounds emitted during 60 minutes of recording by tomato and tobacco plants under two treatments, drought stress and cutting. Three control groups were used – empty pots, and two groups of untreated plants: self-control – the same plants before treatment; and neighbors-control – untreated plants that shared the acoustic box with treated plants. All treatment groups emitted significantly more sounds (p<e-7, Wilcoxon test) than all control groups (treated: $\mathrm{Mean}_{\mathrm{Tomato-Cut}} = 15.2 \pm 2.6$, $\mathrm{Mean}_{\mathrm{Tobacco-Cut}} = 21.1 \pm 3.4$, $\mathrm{Mean}_{\mathrm{Tomato-Dry}} = 35.4 \pm 6.1$, $\mathrm{Mean}_{\mathrm{Tobacco-Dry}} = 11.0 \pm 1.4$), self-control ($\mathrm{Mean}_{\mathrm{self}}<1$ for all) and neighbors control ($\mathrm{Mean}_{\mathrm{neighbors}}<1$ for all). The system did not record any sound from pots without plants during the experiments ($\mathrm{Mean}_{\mathrm{pots}}=0$). $20 \leq n \leq 30$ plants for all groups. (b) Examples of time signals of sounds emitted by: a drought stressed tomato, a drought stressed tobacco, a cut tomato, and a cut tobacco. (c) The spectra of the sounds from (b).

Can we identify the condition of a plant based on the acoustics of the sounds it emits? To test this, we trained a regularized machine learning classifier. We divided the sounds to four groups in a 2X2 design, with two plant types – tomato and tobacco, and two treatments – drought or cutting. The treatments were applied to the plants before the beginning of the recording. The binary classifier was trained to separate two equal-size groups ("pair") in each comparison (Tomato-Dry vs Tomato-Cut; Tobacco-Dry vs Tobacco-Cut; Tomato-Dry vs Tobacco-Dry; Tomato-Cut vs Tobacco-Cut). For cross validation, the model was tested only on plants that were not a part of the training process (see Methods for more details).

The classifier achieved ~70% accuracy for each of the four pairs (Fig. 3b red line), significantly better than random ($p<e{-}13$ for each pair, see methods). The same classifier was trained to discriminate between the electrical noise of the system (see Methods) and the sounds emitted by either tobacco or tomato plants, and achieved more than 98% accuracy for both (Fig. 3b). We used Support Vector Machine (SVM) as the classifier and scattering network (Spangler 1988) for feature extraction. The results were robust to the dimension of the descriptors and the scattering network specific parameters (Fig. S2). The results were also significantly better than random when we used MFCC (Ellis 2005) as the input features ($p<e{-}4$, see methods) and even when we only used 4 basic acoustic features (Acevedo, Corrada-Bravo et al. 2009, Giannakopoulos and Pikrakis 2014) the results were significantly better than random for 5 of the pairs ($p< e{-}4$; Fig. 3b).

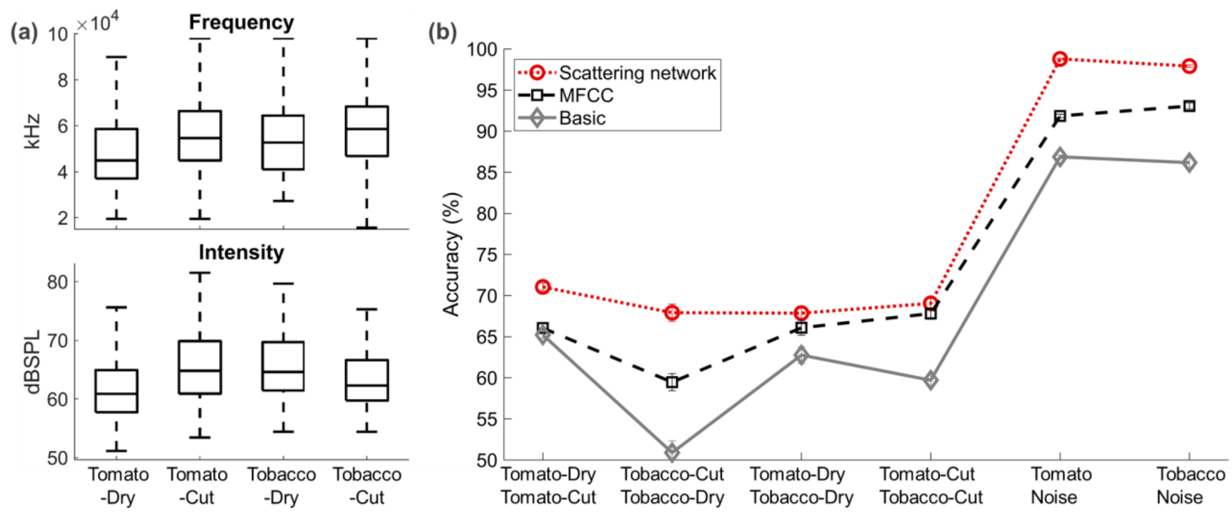

Figure 3. The plant condition can be detected from a distance just by listening to its sound emissions. (a) The recorded sounds intensity peak and the max energy frequency for the four groups – drought stressed tomato plants, cut tomato plants, drought stressed tobacco plants and cut tobacco plants. (b) The accuracy of sound classification achieved by different feature extraction methods, with SVM classifier. The best results were obtained using scattering network method for feature extraction (red line) – significantly better than when we use MFCC or Basic methods for feature extraction for all the pairs ($P<0.05$, $P<$ e-6 correspondingly, Wilcoxon sign rank test). Training set size of the two groups in each pair was equal (400< sounds for each pair, see Table S2).

Discussion

Our results demonstrate for the first time that plants emit remotely-detectable airborne sounds and do so particularly under stress (Fig. 2a). The plant emissions that we report, in the ultrasonic range of ~20-100 kHz, could be detected from a distance of 3-5m (see Methods), by many mammals and insects (when taking their hearing sensitivity into account, e.g., mice (Heffner and Heffner 1985) and moth (Fullard, Dawson et al. 2003)). Moreover, we succeeded in differentiating between sounds emitted in two different stress conditions – dry and cut (Fig. 3b) – with precision of ~70% using supervised machine learning methods. These findings can alter the way we think about the Plant Kingdom, which has been considered to be almost silent until now (Gagliano 2012).

Our work can be extended in several ways. First, plant sound emissions can be tested outdoors. For that, the classifiers would need to separate 'regular outdoor sounds' from plant sounds. However, note that the plants sounds we recorded are all in the ultrasonic range, which is overall quieter than the audible range (Brown and Waser 2017). Second, our results can be generalized to other species of plants from different families. In a preliminary study we successfully recorded sounds from additional plants from different taxonomic families such as *Mammillaria spinosissima* cactus and *Henbit deadnettle* (Fig. S3). We thus expect that many plants have the ability to emit sounds, but the exact characteristics of these sounds, and the similarity between groups, are yet to be identified. Third, future studies could explore the sounds emitted under different plant states, including other stress conditions such as disease, cold, herbivores attack, radiation, and light, and other life stages, such as flowering and fruit bearing. Once a large library of plant sounds is constructed, it could be analyzed by modern tools to obtain additional insights.

A possible mechanism that could be generating the sounds we record is cavitation – the process whereby air bubbles form and explode in the xylem (Tyree and Sperry 1989, Cochard, Badel et al. 2013). Cavitation explosions have been shown to produce vibrations similar to the ones we recorded (Tyree and Sperry 1989, Cochard, Badel et al. 2013) , but it has never been tested whether these sounds are transmitted through air at intensities that can be sensed by other organisms. Regardless of the specific mechanism generating them, the sounds we record carry information, and can be heard by many organisms. If these sounds serve for communication a plant could benefit from, natural selection could have favored traits that would increase their transmission.

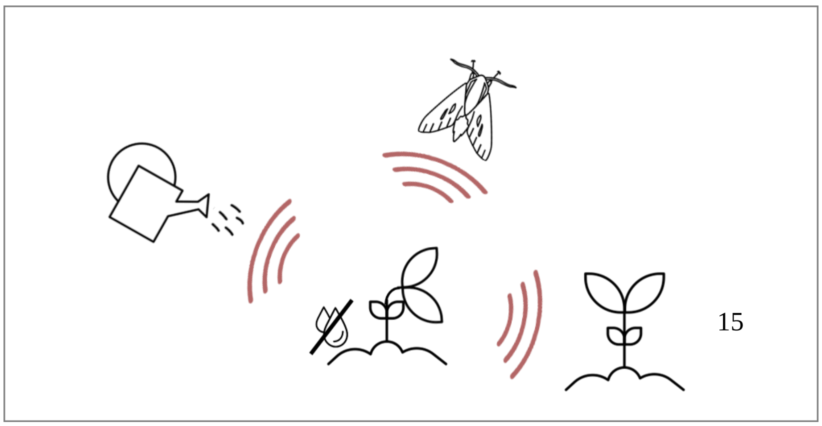

Figure 4. Who can potentially benefit from listening to plants? An illustration of the potential benefits of listening to sounds emitted by a drought stressed plant: (i) A neighbor plant can be alert for drought (ii) A flying moth looking for a host plant can sense plant stress and modify its behavior accordingly (iii) A farmer can use this information to update his irrigation plan.

We have shown that plants sounds can be effectively classified by simple machine learning algorithms. We thus suggest that other organisms may have evolved to classify these sounds as well, and respond to them (Fig. 4). For instance, many moths – some of them using tomato and tobacco as hosts for their larvae (Liu, Li et al. 2004, Specht, de Paula-Moraes et al. 2015) – can hear and react to ultrasound in the frequencies and intensities that we recorded (Spangler 1988, Miller and Surlykke 2001, Fullard, Dawson et al. 2003). These moths may potentially benefit from avoiding laying their eggs on a plant that had emitted stress sounds. We hypothesize that even some predators may use the information about the plant's state to their benefit. For example, if plants emit sounds in response to a caterpillar attack, predators such as bats (Wilson and Barclay 2006) could use these sounds to detect these plants (Jones 1999) and prey on the herbivores, thus assisting the plant. The same sounds may also be perceived by nearby plants. Plants were already shown to react to sounds (Jeong, Shim et al. 2008, Hassanien, HOU et al. 2014, Ghosh, Mishra et al. 2016, Mishra, Ghosh et al. 2016) and specifically to increase their drought tolerance in response to sounds (Jeong, Cho et al. 2014, López-Ribera and Vicient 2017). We speculate that plants could potentially hear their drought stressed or injured neighbors and react accordingly.

Finally, plant sound emissions could offer a novel way for monitoring the crops water state – a question of crucial importance in agriculture (Playán and Mateos 2006). More precise irrigation can save up to 50% of the water expenditure and increase the yield , with dramatic economic implications (Sadler, Evans et al. 2005, Playán and Mateos 2006). In times when more and more areas are exposed to drought due to climate change (Allen and Breshears 1998), while human population and consumption keep increasing (Mueller, Gerber et al. 2012), efficient water use becomes even more critical, for both food security and ecology.

Conclusion

We demonstrate for the first time that stressed plants emit remote detectable sounds, similarly to many animals, using ultrasound clicks not audible to human ears. We also found that the sounds contain information, and can reveal plant state. The results suggest a new modality of signaling for plants and imply that other organisms could have evolved to hear, classify and respond to these sounds. We believe that more investigation in the plant bioacoustics field, and particularly in the ability of plants to emit and react to sounds under different conditions and environments, will reveal a new pathway of signaling, parallel to VOCs, between plants and their environment.

Materials and Methods

Plants materials and growth conditions

Tomato – *Solanum lycopersicum* ‘Hawaii 7981’ (Scott, Jones et al. 1995) – and tobacco – *Nicotiana tabacum* ‘Samsun NN’ – were used in all the experiments. All the plants were grown in a growth room at 25 °C and kept in long-day conditions (16 h day, 8 h night). The plants were tested in the experiments 5-7 weeks after germination.

Recording protocol

The recordings were performed in a 50 × 100 × 150cm^3 acoustically isolated box tiled with acoustic foam on all sides to minimize echoes. Two cable holes, 2 cm radius each, were located in two corners of the box and covered with PVC and acoustic foam. Inside the acoustic box were only the recorded plants, 6 microphones, and an UltraSoundGate 1216H AD converter (Avisoft). The PC and all the electricity connections were in the room outside the acoustic box. Two USB cables connected the PC to the 1216H device inside the box, through the holes. There was no light inside the acoustic box.

The recordings were performed using a condenser CM16 ultrasound microphone (Avisoft), digitized using an UltraSoundGate 1216H A/D converter (Avisoft), and stored onto a PC. The sampling rate was 500 KHz, and we used a high-pass filter of 15 KHz built-in the system. A recording started only when triggered with a sound which exceeded 2% of the maximum dynamic range of the microphone. Two microphones were directed at each plant stem, from a distance of 10 cm. Only sounds that were recorded by both microphones were considered as "plant sounds" in the analysis afterwards. The frequency responses of the microphones can be found in the Avisoft website: http://www.avisoft.com.

Data processing

Data processing was performed off-line using a matlab code we developed (MATLAB 8.3, The MathWork Inc.), with the following steps: 1. Identifying the microphone that had recorded the highest intensity peak at the moment recording started. 2. Selecting the sounds that were detected by two microphones oriented at the same plant at the same time, and saving them for further analysis. Throughout the experiments, not a single detection of a sound was observed simultaneously at different plants. "Noise" sounds were obtained when the box included only acoustic equipment without plants or pots, and each "noise" was detected by one microphone only. These noises probably resulted from electrical noise of the acoustic equipment.

Drought stress experiment

Each plant was recorded twice: first before drought treatment ("self-control"), and again after it. In the first recording, all the plants were healthy and their soil was moist. Then, for 4-6 days, half of the plants were watered while the other half were not, until the soil moisture in the pots of un-watered plants decreased below 5%. Then, the plants were recorded again at the same order. In each recording session three plants were recorded simultaneously for one hour and each triplet of plants included at least one watered and one un-watered plant to allow “neighbors-control” – watered plants that were recorded while sharing the acoustic box with un-watered plants. Soil moisture content was recorded using a hand-held digital soil moisture meter - Lutron PMS-714.

Cut stress experiment

The experiment followed the experimental design of the drought stress experiment described above, but drought stress was replaced with cutting of the plant. Here the pot soil was kept moist for all the plants throughout the experiment. The plants included in the treatment group were cut with scissors close to the ground right before the recording started. The severed part of the plant, disconnected from the roots, was recorded. We used the same controls of the drought stress experiment.

Classifying sounds

Our classification method was composed of two main stages. First, we extracted various acoustic features from the raw recorded signals. Second, we trained a model to classify plant sounds into classes based on the feature representation obtained in the first stage. We used three methods of feature extraction: (a) Deep scattering Network, as described in Andén and Mallat (Andén and Mallat 2014), red dotted line in Fig. 3b. This method extends MFCC while minimizing information loss. We used the implementation by ScatNet (Sifre, Kapoko et al. 2013), with Morlet wavelets. The results were robust to the dimension of descriptors and the scattering network specific parameters: number of layers used; time support of low pass filter; and Q-

Factor (Fig. S2). The values of the specific parameters used in this work are shown at Table S1. (b) MFCC feature extraction (dashed black line in Fig. 3b). We used the Ellis Dan implementation (Ellis 2005). (c) Basic features. The basic features we used were energy, energy entropy, spectral entropy, and maximum frequency (gray line in Fig. 3b) (Acevedo, Corrada-Bravo et al. 2009, Giannakopoulos and Pikrakis 2014). We used SVM with Radial kernel with the LIBSVM implementation as classifier. We used Z-score for normalization and PCA to reduce the dimensionality of the problem. We used only the training set to choose the number of components.

During the training process we leave all the emitted sounds of one plant out for cross validation. Then we constructed the training set such that the two compared groups would be at the same size. We repeated the process so that each plant constructed the testing group exactly one time. The accuracy of the classification was defined as the percentage of correct labeling over the total size of the testing set (Huang, Yang et al. 2009, Noda, Travieso et al. 2017). The numbers of plants in each group are shown at the Table S3.

Statistical analysis

For statistical analysis of the number of sound emissions for the treatment and the control groups (Fig. 2a) we used the Wilcoxon rank-sum test.

To compare our classifier to random result (Fig. 3b), we used the binomial probability distribution function (PDF) and calculate the probability to get the classifier accuracy or higher randomly for each group.

To compare the results obtained when using scattering network for feature extraction to the results obtained when using MFCC or basic feature extraction methods (Fig. 3b), we used Wilcoxon sign rank test.

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Supporting Information

Fig. S1 Examples for spectrograms of sounds which emitted by stressed plants.

Fig. S2 Comparison of different scattering network configurations.

Fig. S3 Recorded sounds from different plants.

Table S1 Parameters used in the feature extraction phase.

Table S2 Pairs total sizes.

Table S3 Groups sizes.