Biophysics

AIMS Biophysics, 4(4): 576-595.
DOI: 10.3934/biophy.2017.4.576
Received: 27 July 2017
Accepted: 29 September 2017
Published: 17 October 2017

http://www.aimspress.com/journal/biophysics

Research article

Electrotonic signal transduction between *Aloe vera* plants using underground pathways in soil: Experimental and analytical study

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Abstract: Plants communicate with other plants using different pathways: (1) volatile organic compounds' (VOC) emission and sensing; (2) mycorrhizal networks in the soil; (3) the plants' rhizosphere; (4) electrostatic or electromagnetic interactions; (5) roots of the same species can sometimes naturally graft. Here we show that there is an additional pathway for electrical signal transduction between neighboring plants: fast underground electrical signal propagation between roots through the soil. The mathematical model of electrical signal transduction between plants and the analytical study are supported by experimental data. The pulse train, sinusoidal and a triangular saw-shape voltage profiles were used for electrostimulation of plants and underground electrotonic signal transmission between plants. Electrostimulation of a leaf in *Aloe vera* by 1.5 V D-batteries or by a function generator induces electrotonic potentials propagation in the electrostimulated plants and the neighboring plants. The amplitude and sign of electrotonic potentials in both electrostimulated and neighboring *Aloe vera* plants depend on the amplitude, rise and fall of the applied voltage. Electrostimulation by a sinusoidal wave from a function generator induces an electrical response in leaves with a phase shift. Experimental results show cell-to-cell electrical coupling and existence of electrical differentiators in the leaves of *Aloe vera*. Electrostimulation is an important tool for the evaluation of mechanisms of communication between plants.

Keywords: *Aloe vera*; biophysics; electrical differentiator; electrostimulation; electrotonic potential; cell-to-cell electrical coupling; plant-to-plant electrical coupling

Abbreviations:

C	capacitance;
CCCP	carbonylcyanide-3-chlorophenylhydrazone;
DAQ	data acquisition;
FCCP	carbonylcyanide-4-trifluoromethoxyphenyl hydrazine;
R	resistance;
V	voltage;
V_{in}	input voltage;
VOC	volatile organic compounds

1. Introduction

A monocot *Aloe vera* (L.) is a member of the *Asphodelaceae* (*Liliaceae*) family with crassulacean acid metabolism (CAM) and has been used for thousands of years in medicine, cosmetics, and as an ornamental plant. The succulent, non-fibrous leaves of the *Aloe vera* grow from the base in the rosette pattern. In *Aloe vera*, their stomata are open at night and closed during the day.

Plants can communicate with other plants using different pathways above ground such as volatile organic compounds (VOC) emission and sensing [1,2]; electrostatic induction; electromagnetic interactions [3–7]. There is underground communication between plants: roots grafting; mycorrhizal networks in the soil and/or the plants' rhizosphere [8–12].

Mycorrhizal symbiosis between plants and fungi is one of the most well-known plant-fungus associations, which is important for plant growth in many ecosystems. Mycorrhizal fungi can connect individual plants together and mediate transfer of carbohydrates, water, nitrogen, phosphorus, defense compounds, and other nutrients and minerals between plants through so called common mycorrhizal networks [12,13,14].

Biophysical and electrophysiological phenomena in plants have attracted researchers since the eighteenth century [15–18]. The cells of many biological organs generate electrical potentials that result in the flow of electric currents. It is well known that electrostimulation of plants can induce activation of ion channels and ion transport, gene expression, enzymatic systems activation, electrical signaling, plant movements, enhanced wound healing, plant-cell damage and influence plant growth [19]. The electrostimulation by bipolar sinusoidal or triangular periodic waves induce electrical responses in plants, fruits, roots and seeds with fingerprints of generic memristors [7]. There are two mayor types of electrical signaling in plants and animals: action potentials and electrotonic potentials. The action potential can propagate over the entire length of the cell membrane and along the conductive bundles of tissue with constant amplitude, duration, and speed [7]. Passive electrotonic potentials in plants exponentially decrease with distance [19,20,21]. Amplitude of electrotonic potentials depends on the size of the stimulus.

In small neurons, exponentially decreasing electrical potentials are referred to as electrotonic potentials. Electrotonic potentials can induce action potentials in small neurons, dendrites and in plants. The electrotonic potentials in plants were recently discovered [19,20,21]. Electrostimulation of electrical circuits in *Aloe vera* and other plants induce electrotonic potentials with amplitude exponentially decreasing along a leaf or a stem [19,20,21]. Mechanical stimulation of trigger hairs in the Venus trap induces action potential propagating between the trigger hairs in a lobe and electrotonic potentials in the lower leaf of the Venus flytrap [21].

Recently, we analyzed anisotropy and nonlinear properties of electrochemical circuits in the leaves of *Aloe vera* [19,22]. There is a strong electrical anisotropy of the *Aloe vera* leaf. In the direction across the conductive bundle, the behavior of the system is completely passive and linear like in a regular electric circuit with a constant resistance. Conductance parallel to vascular bundles are two orders of magnitude higher than the perpendicular direction [22].

Electrical signals in plants can propagate along the plasma membrane on long distances in vascular bundles, and on short distances in plasmodesmata and protoxylem [23,24].

Soil is a good electrical conductor between neighboring plants [25]. The soil electrical resistivity depends on moisture, cation exchange capacity, porosity, pore size distribution, solute concentration, temperature and chemical content. The resistivity ρ (Ωm) is defined as follows:

$$\rho = R \times (S/L) \tag{1}$$

with R being the electrical resistance (Ω), L the length of the cylinder (m) and S its cross-sectional area (m^2). The resistivity usually varies between 1 Ωm for saline soil to 100 kΩm for dry soil overlaying crystalline rocks [26].

There is no information in literature about possible underground electrical communication between plants through soil. The main goal of this article is to investigate possibilities of fast underground electrical signal transduction between plants.

2. Materials and Method

2.1. Plants

Fifty *Aloe vera* L. plants were grown in clay pots with sterilized potting soil. Plants were exposed to a 12:12 hr light/dark photoperiod at 21 ℃ . *Aloe vera* plants had 20–35 cm leaves. Volume of soil was 1.0 L. The average air humidity was 40%. Irradiance was 700–800 µmol photons $m^{-2}s^{-1}$ PAR at plant level. All experiments were performed on healthy adult specimens.

2.2. Chemicals

Daconil containing 0.087% of chlorothalonil (GardenTech, Colorado Springs, USA) known also as 2,4,5,6-tetrachloroisophthalonitrile, Bravo, Echo, Exotherm, Termil, Forturf, Mold-Ex, Nopcocide N-96, Ole, Pillarich, Repulse, and Tuffcide, was used as antifungal treatment of soil in control experiments. It may also be used to kill mildew, bacteria, algae, and insects.

2.3. Electrodes

All measurements were conducted in the laboratory at 21 ℃ inside a Faraday cage mounted on a vibration-stabilized table. Teflon coated silver wires (A-M Systems, Inc., Sequim, WA, USA) with a diameter of 0.2 mm were used for preparation of non-polarizable electrodes. Reversible Ag/AgCl electrodes were prepared in the dark by electrodeposition of AgCl on 5 mm long silver wire tip without Teflon coating in a 0.1 M KCl aqueous solution. The anode was a high-purity silver wire and the cathode was a platinum plate. Electrical current in the electrolytic cell was limited to 1 mA/cm^2 of the anode surface. Stabilization of electrodes was accomplished by placing two Ag/AgCl electrodes in a 0.1 M KCl solution for 24 hours and connecting a short circuit between them. The response time of Ag/AgCl electrodes was less than 0.1 µs. Identical Ag/AgCl electrodes were used as working and reference electrodes for measurements of potential differences in plants.

Platinum electrodes were used for plant electrostimulation and prepared from Teflon coated platinum wires (A-M Systems, Inc., Sequim, WA, USA) with a diameter of 0.076 mm. We allowed the plants to rest for 2 hours after electrode insertion. All electrodes were inserted along the vascular bundles of a leaf. In control experiments, electrodes were inserted directly to soil.

2.4. Data acquisition

Experimental setup is shown in Figure 1. High speed data acquisition was performed using microcomputers with simultaneous multifunction I/O plug-in data acquisition board NI-PXI-6115 (National Instruments, Austin, TX, USA) interfaced through a NI SCB-68 shielded connector block to Ag/AgCl and Pt electrodes. The system integrates standard low-pass anti-aliasing filters at one half of the sampling frequency.

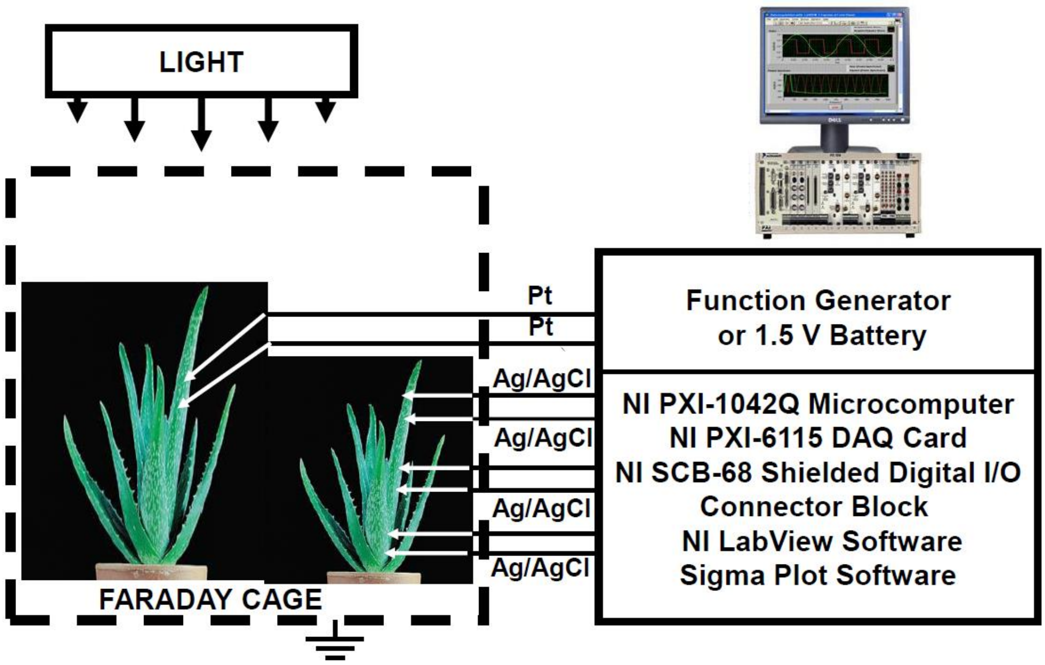


Figure 1. Experimental setup. Function generator or 1.5 V battery connected to platinum electrodes were used for electrostimulation.

2.5. Plant electrostimulation

We used two methods of plant electrostimulation: the function generator or the 1.5 V D-batteries. The function generator FG300 (Yokagawa, Japan) was interfaced to the NI-PXI-1042Q microcomputer and used for the electrostimulation of plants (Figure 1). The function generator gives many options for the electrostimulation: shapes, duration, and frequency of stimulation.

2.6. Images

A photo camera Nikon D3x with AF-S Micro Nikkor 105 mm 1:2.8 G ED VR lenses was used for the photography of plants.

2.7. Statistics

All experimental results were reproduced at least 25 times using different *Aloe vera* plants. Software SigmaPlot 12 (Systat Software, Inc., San Jose, CA, USA) was used for statistical analysis of experimental data.

3. Results

3.1. Experimental study

3.1.1. Experiment 1

Following insertion of the electrodes, the plants were allowed to rest until a stable potential difference was obtained between electrodes. Electrostimulation of a leaf in one of the *Aloe vera* plant by a 1.5 V D-battery (Figure 2A) or by square pulse trains with amplitude of ±1.5 V from a function generator (Figure 2B) induces electrical signals in leaves of another *Aloe vera* plant if both plants located in the same pot.

Since results of electrostimulation of *Aloe vera* leaves by a function generator or battery are the same, this phenomenon is not caused by a possible electrical coupling between data acquisition system and a function generator through power supply and ground. Amplitude of electrotonic potentials depends on amplitude and polarity of a stimulus. Amplitude decreases exponentially along a leaf with distance from electrostimulating electrodes [19,27]. Electrotonic potential propagates underground through soil from one plant to another plant.

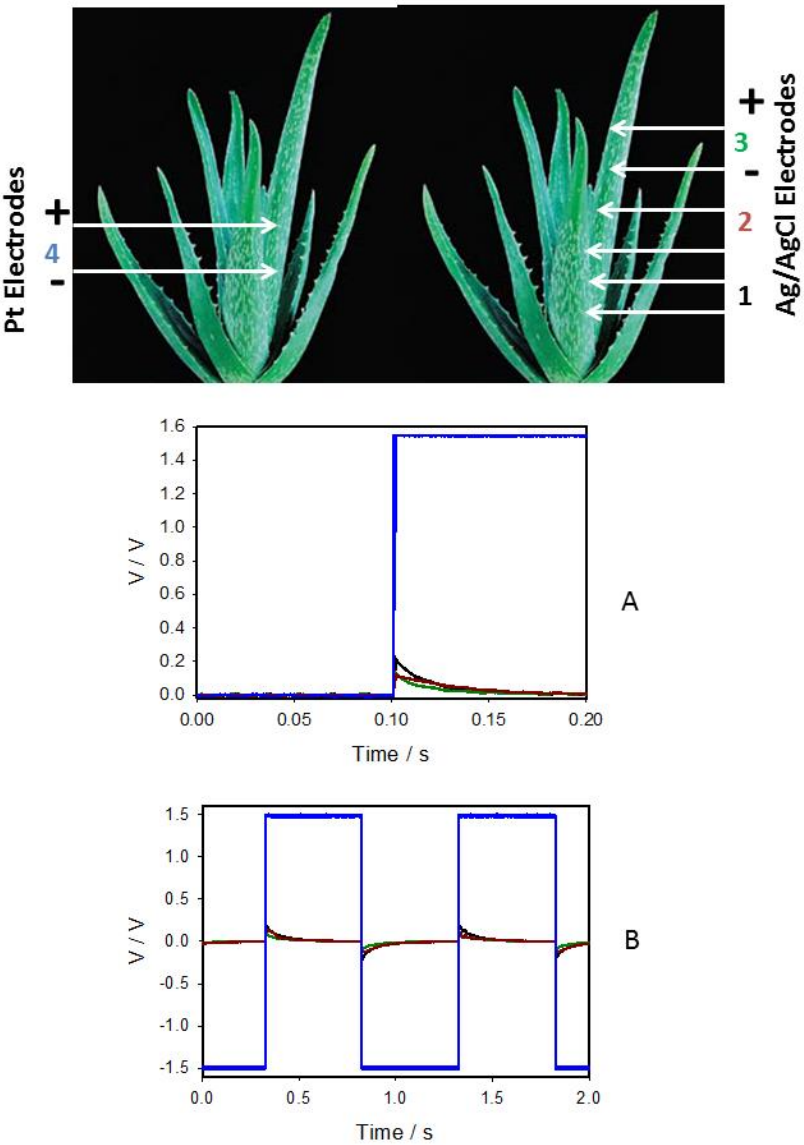


Figure 2. Electrical responses in *Aloe vera* leaf induced by 1.5 V electrical battery (A) or by a ±1.5 V square pulse wave from a function generator (B) connected to platinum electrodes in another plant located in the same ceramic pot. Distance between plants was 5 cm. Measurements were performed at 50,000 scans/s with low pass filter at 25,000 scans/s (B).

3.1.2. Experiment 2

Wet soil is a good electrical conductor and electrostimulation of soil by the pulse train, sinusoidal and a triangular saw-shape voltage profiles from a function generator connected to platinum electrodes induces propagation of the electrical waves without a phase shift in soil (Figure 3). Amplitude of electrical waves decreases with distance from platinum electrodes.

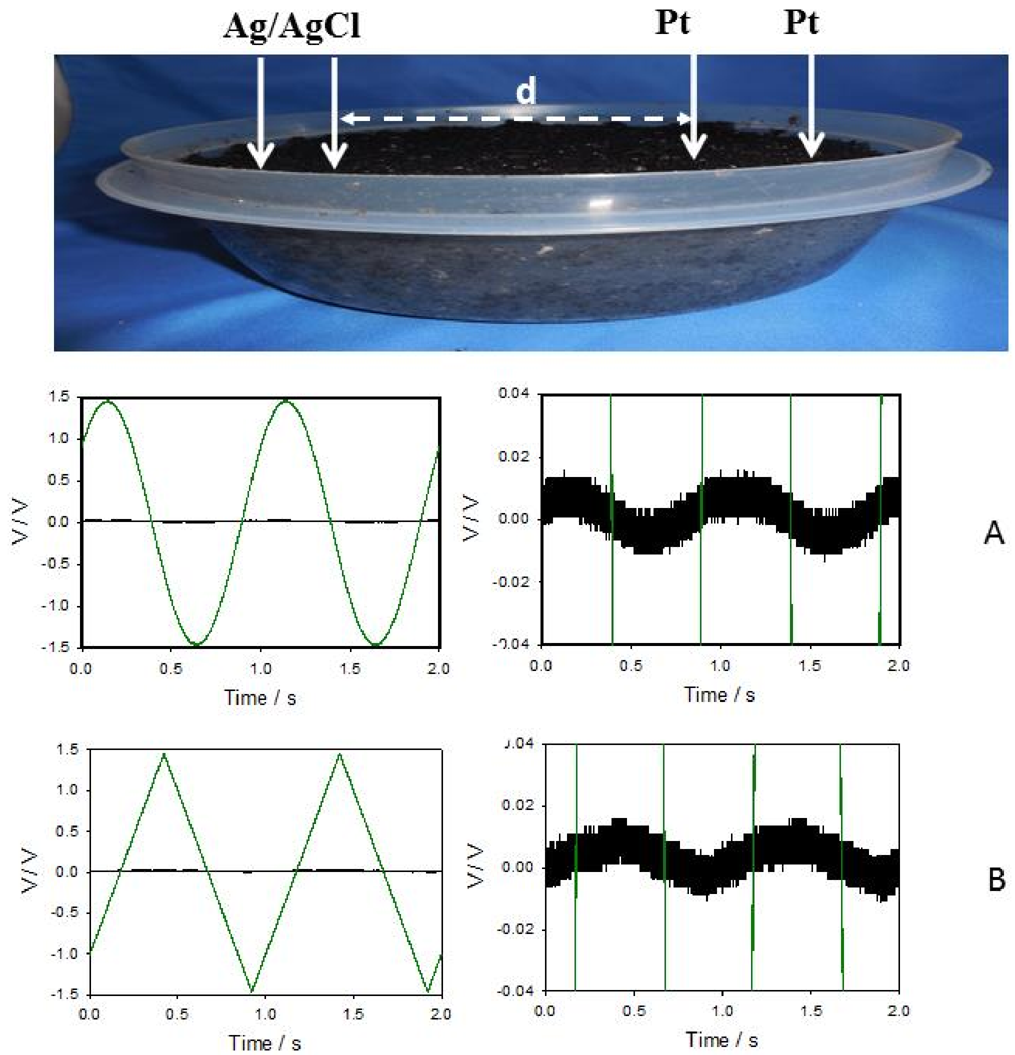


Figure 3. Electrostimulation of soil by a ±1.5 V sinusoidal wave (A) or triangular wave (B) from a function generator connected to platinum electrodes immersed to soil. Measurements were performed at 50,000 scans/s with low pass filter at 25,000 scans/s. Distance between Pt electrodes was 2 cm, distance between Ag/AgCl electrodes was 3 cm; d = 5 cm.

3.1.3. Experiment 3

Electrostimulation of soil by a sinusoidal bipolar wave induces electrical responses with a phase shift in *Aloe vera* plant (Figure 4B).

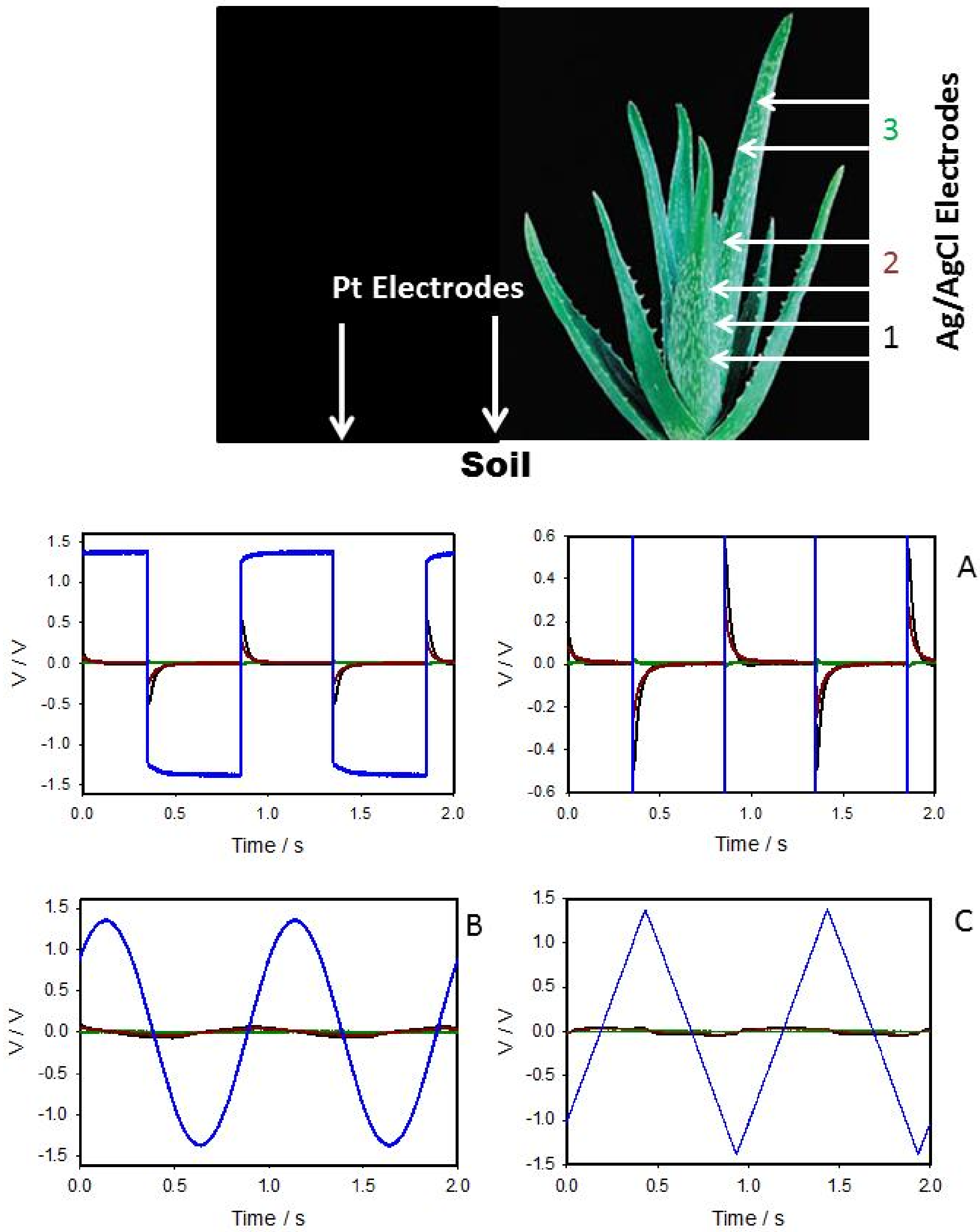


Figure 4. Electrical responses in *Aloe vera* leaf induced by a ±1.5 V square pulse wave (A), sinusoidal (B) or triangular (C) waves from a function generator connected to platinum electrodes immersed into soil near plant. Measurements were performed at 50,000 scans/s with low pass filter at 25,000 scans/s.

3.1.4. Experiment 4

If two different *Aloe vera* plants are grown in the same pot, there is a possibility of electrical communication between both plants through wet soil as an electrical conductor between plants (Figure 2). If two different *Aloe vera* plants are grown in different pots without electrical connection between them, there is no electrical coupling between electrical networks of both plants (Figure 5). It means that volatile organic compounds' emission and sensing are not responsible for communications between *Aloe vera* plants induced by electrostimulation of a leaf of *Aloe vera*.

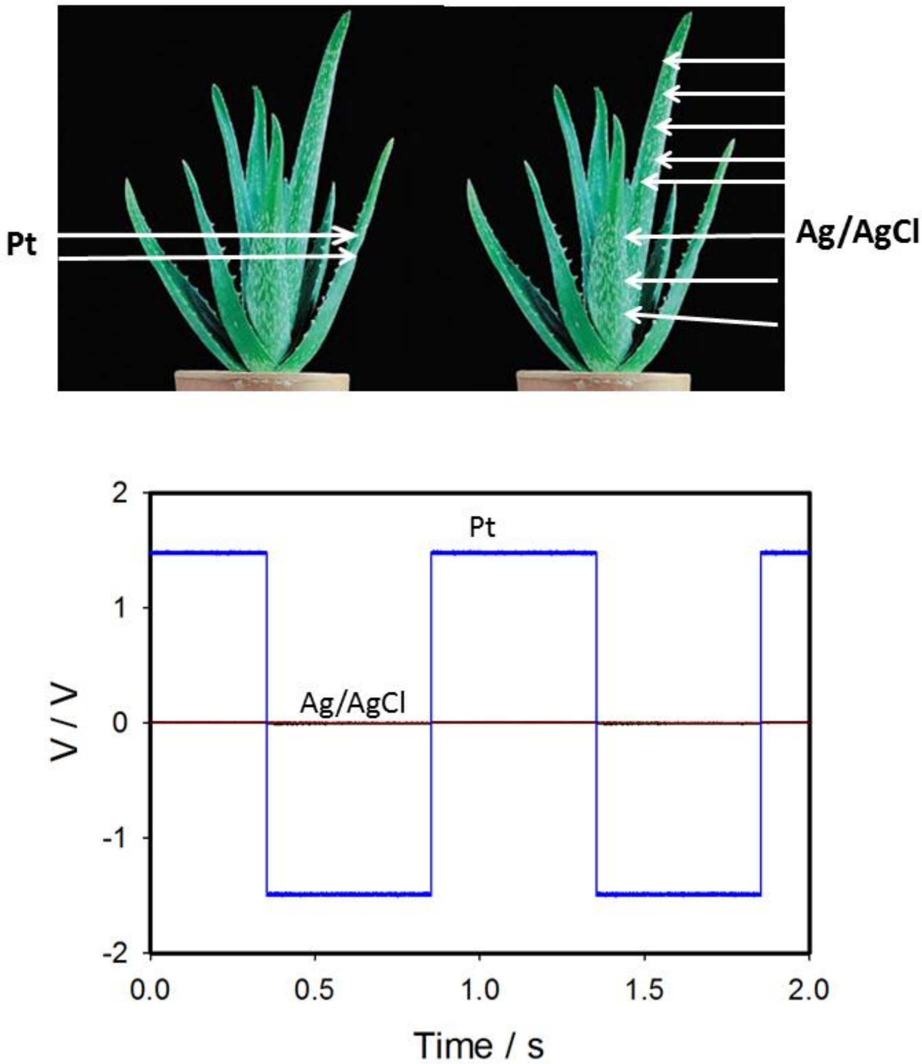


Figure 5. Electrical responses in *Aloe vera* leaf induced by a ±1.5 V square pulse wave from a function generator connected to platinum electrodes in another plant located in another isolated ceramic pot. Distance between plants was 5 cm. Measurements were performed at 50,000 scans/s with low pass filter at 25,000 scans/s.

3.1.5. Experiment 5

Fungi can create *mycorrhizal* networks between roots of different plants or trees [11,12,14]. Daconil containing 0.087% of chlorothalonil was used as an antifungal treatment of soil in control experiments (Figure 6). It may also be used to kill mildew, bacteria, algae, and insects. Soil was treated by 5 ml of Daconil 12 hours before electrostimulation and response measurements. Daconil did not influence the electrical responses in *Aloe vera* during electrostimulation by the pulse train (Figure 6), sinusoidal or a triangular saw-shape voltage profiles.

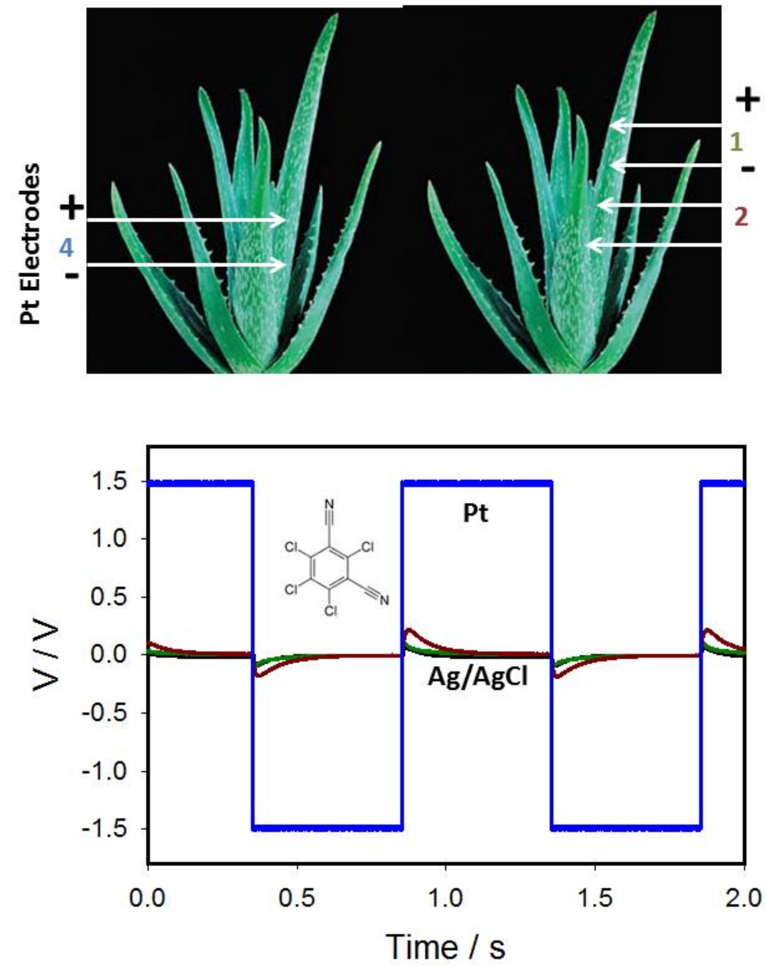


Figure 6. Electrical responses in *Aloe vera* leaf induced by a ±1.5 V square pulse wave from a function generator connected to platinum electrodes in another plant located in the same ceramic pot. Soil between plants was treated by fungicide Daconil 18 hours before electrical measurements. Distance between plants was 5 cm. Measurements were performed at 50,000 scans/s with low pass filter at 25,000 scans/s.

3.2. Mathematical modeling and simulations

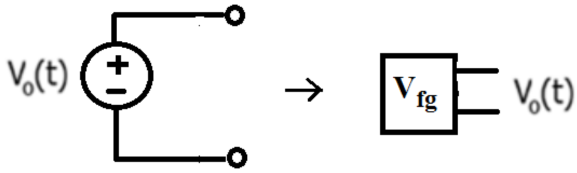
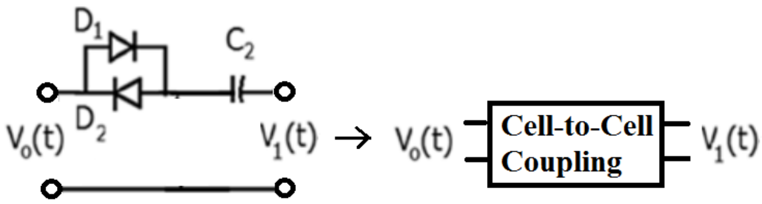
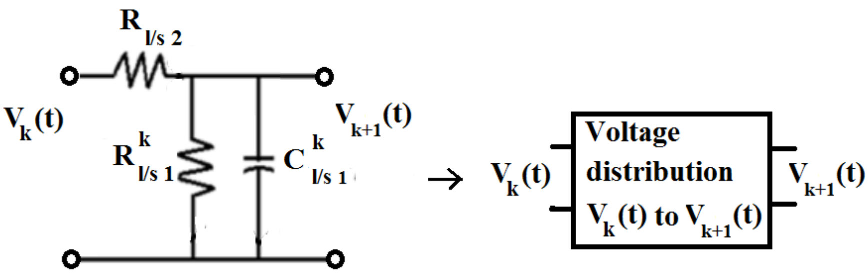
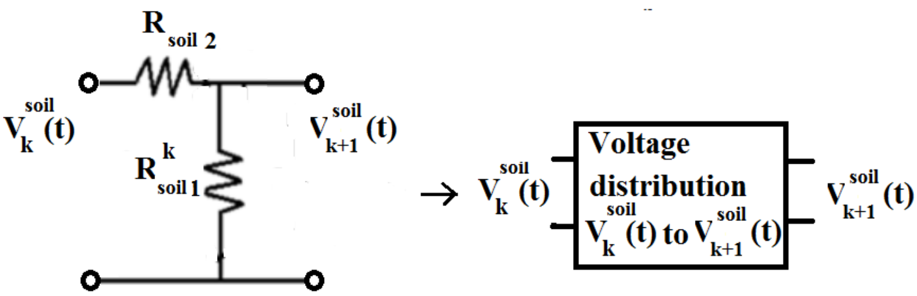
The mathematical models are derived based on the classical *cable theory* that has been originally applied to the study of potential propagation in an axon by Hodgkin and Rushton [28]. In this work applying the cable theory-based mathematical model has been used to describe the dynamics of the electrotonic potentials in plants connected through the soil.

The mathematical models describe the Experiments 1, 2, 3, specifically:

1. Electrostimulation of a leaf in one of *Aloe Vera* plant from a function generator; induces electrical signals in leaves of another *Aloe Vera* plant if both plants located in the same pot;
2. Electrical stimulation of soil;
3. Electrical stimulation of a single plant *Aloe Vera* through soil.

These mathematical models were obtained in terms of block diagrams and respective transfer functions.

Table 1. Blocks introduced for the mathematical modeling of the experiments.

<table>
<tr><th>No</th><th>Mathematical modeling</th><th>Block titles</th></tr>
<tr><td>1</td><td>
</td><td>Voltage function generator block</td></tr>
<tr><td>2</td><td>
</td><td>Cell-to-cell coupling block</td></tr>
<tr><td>3</td><td>
</td><td>Voltage distribution along the leaf/stem length</td></tr>
<tr><td>4</td><td>
</td><td>Voltage distribution along the soil length</td></tr>
</table>

The mathematical models of the blocks are derived in a transfer function format:

1. The transfer function of the cascade connection of the blocks 1-2-3:

$$G^k_{1-2-3}(s) = \frac{V_{k+1}(s)}{V_0(s)} = \frac{C_{21} R^k_{l/s2} s}{C^k_{l/s1} C_{21} R^k_{l/s1} R^k_{l/s2} s^2 + \left(C_{21} R^k_{l/s2} + C^k_{l/s1} R^k_{l/s1} + C_{21} R^k_{l/s1}\right) s + 1} \quad (2)$$

2. The transfer function of the block 3:

$$G_3(s) = \frac{V_{k+1}(s)}{V_k(s)} = \frac{R^k_{l/s2}}{C^k_{l/s1} R^k_{l/s1} R^k_{l/s2} s + \left(R^k_{l/s1} + R^k_{l/s2}\right)} \tag{3}$$

3. The transfer function of the block 4:

$$G_4(s) = \frac{V^{soil}_{k+1}(s)}{V^{soil}_k(s)} = \frac{R^k_{soil1}}{R^k_{soil1} + R^k_{soil2}} \tag{4}$$

Where $k = 1,2,3\ldots$, and s is the Laplace variable.

It is worth noting that the derived mathematical model in eq. (2) that involves the block #2 describes linear dynamical processes of electrotonic potentials in the plants. The nonlinear effects presented in the block #2 by the diodes D_1 and D_2 will be added to the mathematical model of the electrotonic potentials in the plants in the following up study.

3.2.1. Simulation set up

The parameters of the blocks involved in the simulations of the Experiments 1, 2, and 3 were selected as [19]:

$$C_{21} = 150 \cdot 10^{-9} F,\ C^1_{l/s1} = 0.2 \cdot 10^{-9} F,\ C^1_{l/s2} = 20 \cdot 10^{-9} F,\ R^1_{l/s1} = 150 \cdot 10^3 \Omega,\ R^1_{l/s2} = 86 \cdot 10^3 \Omega$$

$$C^2_{l/s1} = 0.2 \cdot 10^{-9} F,\ C^2_{l/s1} = 150 \cdot 10^{-9} F,\ R^2_{l/s1} = 220 \cdot 10^3 \Omega,\ R^2_{l/s2} = 86 \cdot 10^3 \Omega$$

$$R^1_{soil1} = 100 \cdot 10^3 \Omega,\ R^2_{soil1} = 790 \cdot 10^3 \Omega$$

Note that the transfer function of the steam/leaf of the *Aloe Vera* 2 is represented by three consecutive Blocks #3, whose parameters are the same.

3.2.2. Experiment 1

The following equivalent electric scheme (block-diagram) is proposed for the Experiment 1:

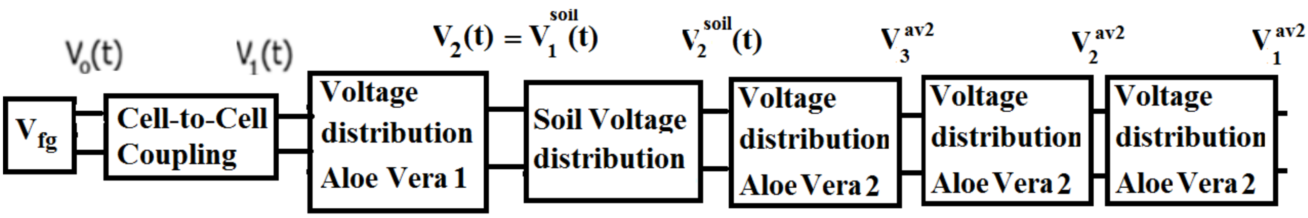


Figure 7. Block diagram for Experiment 1.

Matlab simulations based on eqs. (2)–(4) produced the following plots (Figure 8), where V1 (av2), V2 (av2) and V3 (av2) correspond to the electronic potentials at the points1, 2 and 3 respectively of *Aloe Vera* 2 (see Figure 2).

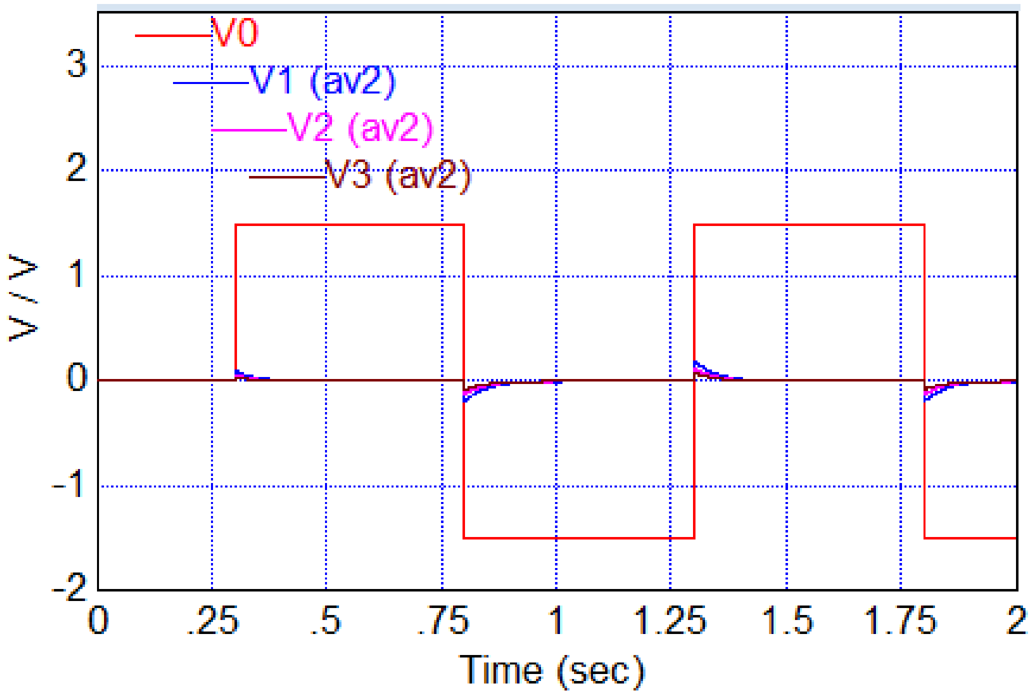


Figure 8. Simulations for the Experiment 1.

3.2.3. Experiment 2

The following equivalent electric scheme (block-diagram) is proposed for the Experiment 2:

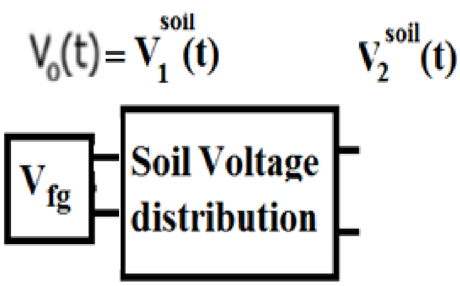


Figure 9. Block diagram for Experiment 2.

Matlab simulations based on eqs. (2)–(4) produced the following plots:

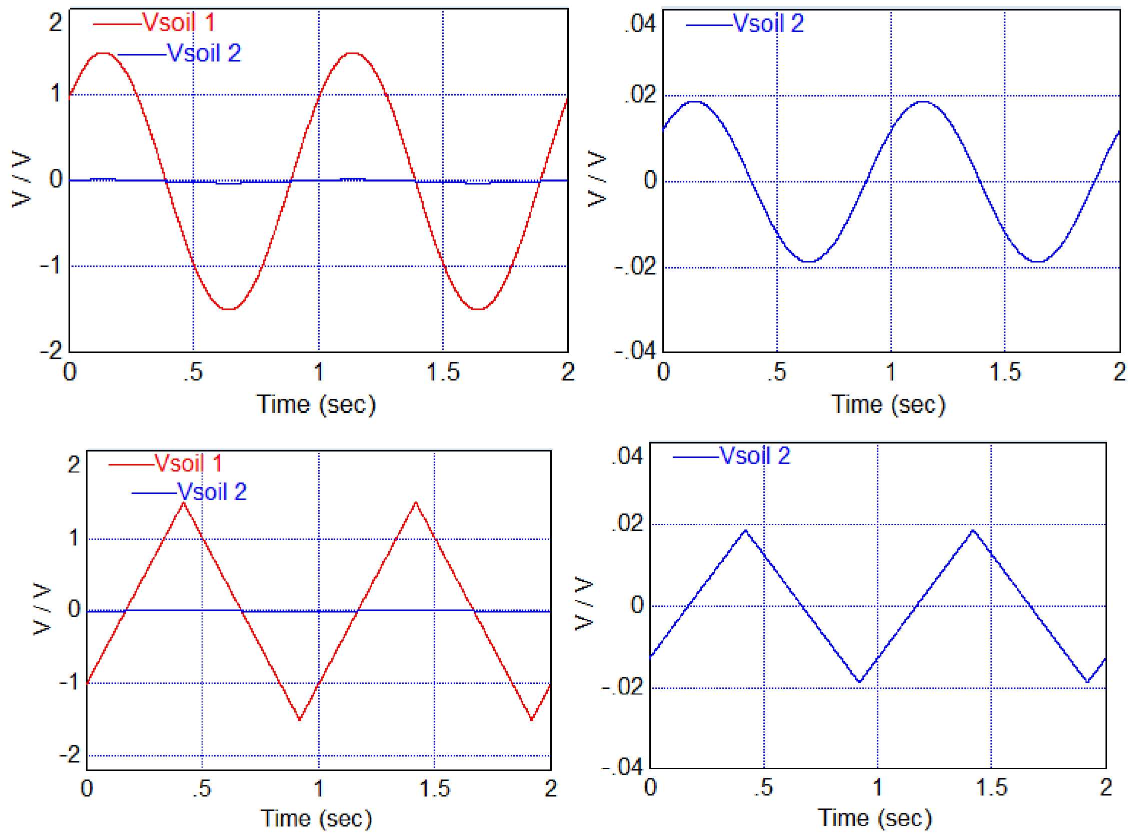


Figure 10. Simulations for the Experiment 2.

3.2.4. Experiment 3

The following equivalent electric scheme (block-diagram) is proposed for the Experiment 3:

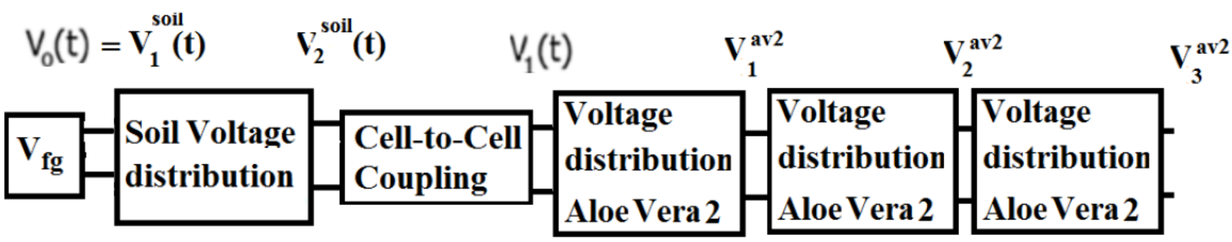


Figure 11. Block diagram for Experiment 3.

Matlab simulations based on eqs. (2)–(4) produced the following plots:

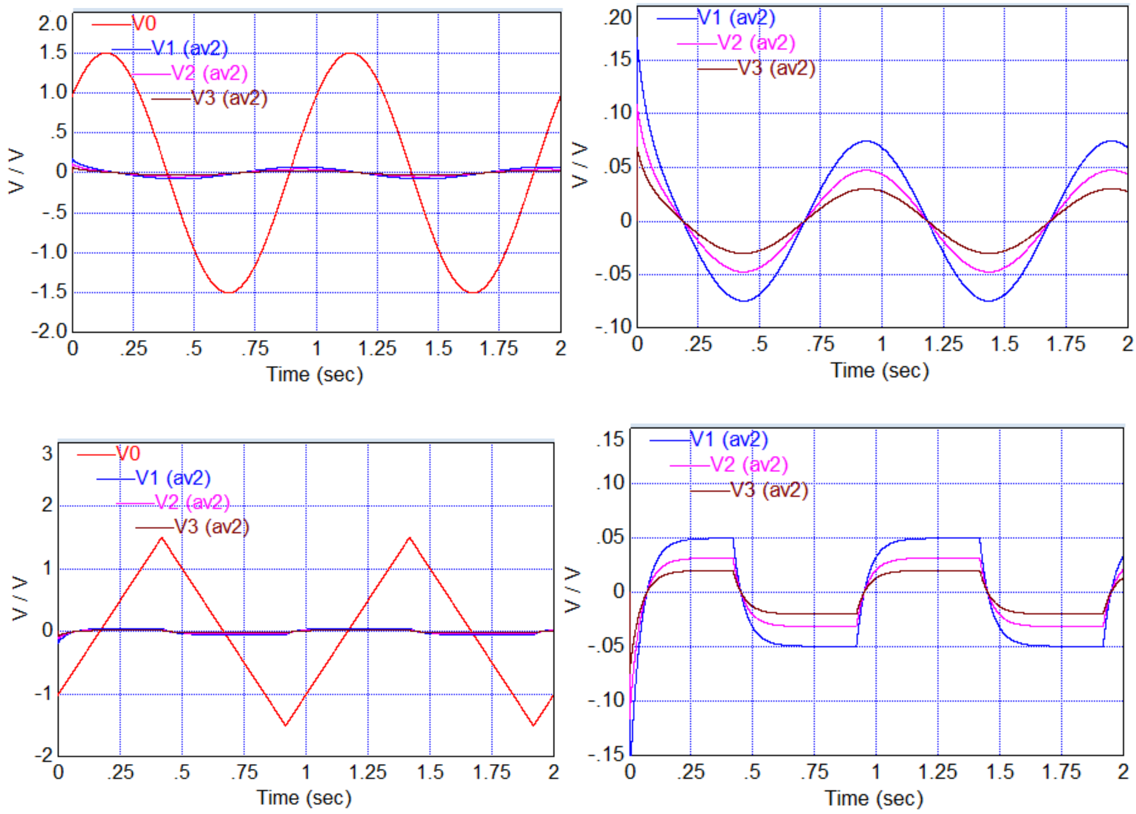


Figure 12. Simulations for Experiment 3.

4. Discussion

Plants communicate with other plants using different pathways: (1) volatile organic compounds' (VOC) emission and sensing; (2) mycorrhizal networks in the soil; (3) the plants' rhizosphere; (4) electrostatic or electromagnetic interactions; (5) roots of the same species can sometimes naturally graft.

Electrostimulation of a leaf in one plant induces propagation of electrical signals along a leaf, root and soil to a different plant (Figure 2). Experimental value of the time constant is equal to 31.1 ms (Median 28.5, Std. Dev. 4.9 ms, Std. Err. 0.87, n = 32). In analytical model the space constant is equal to 1.38. We selected in our previous publications parameters of the electrical circuit to describe experimental results in a single leaf of *Aloe vera*. This set of parameters is very realistic and describes all our results such as kinetics of electrotonic potentials, time constants, the length of the electrotonic potential, etc. We do not change our set of parameters for *Aloe vera* for estimation of different electrical effects in these plants.

Electrical signals can propagate to adjacent excitable cells due to the electrical coupling between plant cells and plasmodesmata, which is the major path for cell-to-cell electrical coupling. This propagation can be either active, representing an action potential, or passive, described as an electrotonic potential. The amplitude of electrotonic potential in plants exponentially decreases with distance. Electrostimulation of electrical networks in plants can induce electrotonic potentials propagation along conductive vascular bundles in a bio-tissue. It is not clear whether electrotonic potentials propagate along a plasma membrane in a phloem or in a xylem.

If the stimulus changes very sharply, the plant's response is very significant and nonlinear: the square impulses initiate electrical responses with shapes completely different from the stimulating voltage, which look like spikes or "action" potentials (Figure 2, Figure 4A). Any stimulation that is not instantaneous, such as a sinusoidal (Figure 4B, Figure 4C) or triangular function, does not induce electrical spikes as responses in the case of square pulses, but the responses are different from stimuli.

This phenomenon shows that electrical networks in plant tissue have electrical differentiators. A differentiator is an electrical circuit that is designed such that the output of the circuit is approximately directly proportional to the rate of change of the input:

$$V(t) = RC\frac{d}{dt}(V_{in}(t) - V(t)) . \tag{5}$$

where V_{in} is input voltage, V is output voltage, R is resistance and C is capacitance.
If

$$\frac{dV(t)}{dt} << \frac{dV_{in}(t)}{dt} \tag{6}$$

then

$$V(t) = RC\frac{d}{dt}V_{in}(t) \tag{7}$$

According to eq. (7), $V_{in} = A\ sin(\omega t)$ yields $V(t) = \omega RCA\ cos(t)$, i.e. the 90° phase shift is expected. The experimental study of the differentiation property of cell-to-cell electrical coupling was reported for the first time in the literature on plant physiology and biophysics in the work [19]. The existence of electrical differentiators and cell-to-cell electrical coupling was demonstrated in the Venus flytrap, *Aloe vera*, *Mimosa pudica* and *Arabidopsis thaliana* [19,20,21,27]. Amplitude and the sign of this response depend on the amplitude of applied voltage and the polarity of electrostimulating electrodes (Figure 2B). The response does not obey the all-or-none rule and it is not an action potential but rather corresponds to the propagating electrotonic potential. Electrical signals in *Aloe vera* are sensitive to various membrane active pharmaceutical agents during electrostimulation [19,20,21,27]. Injection of tetraethylammonium chloride (TEACl) near or between Pt-electrodes decreases the amplitude of electrotonic potential. TEACl is known as a blocking agent of K^+-ion channels [7,27]. We can assume that these voltage-gated ion channels are involved in the generation of electrotonic responses or cell-to-cell electrical coupling in *Aloe vera*. Uncouplers carbonylcyanide-3-chlorophenylhydrazone (CCCP) or carbonylcyanide-4-trifluoromethoxyphenyl hydrazine (FCCP) inhibit electrotonic potentials in the leaf of *Aloe vera* [19,20,21,27]. This effect was also predicted and estimated by our mathematical model [19]. Uncouplers, which are soluble in both water and lipids, permeate the lipid phase of a membrane by diffusion and transfer protons across the membrane, thus eliminating a proton concentration gradient and decreasing the transmembrane resistance and capacitance.

An electrical differentiator used in the analytical model is shown as the block "cell-to-cell electrical coupling in the block diagram derived for the simulation of Experiments 1 and 3. The capacitor used in this block describes the electrical differentiator, while the voltage gated ion channels are modelled as diodes.

Figure 5 shows that there is no electrical communication between *Aloe vera* plants during electrostimulation of a plant leaf if soil surrounded each plant are not electrically connected. It means that such mechanisms as electrostatic induction or electromagnetic interactions in gas phase and/or volatile organic compounds (VOC) emission and sensing are not responsible for fast electrical communication between two *Aloe vera* plants in our experiments. Antifungal treatment of soil by Daconil does not influence on electrical communication between plants (Figure 6). It means that fast underground electrical communication in our experiments is not caused by mycorrhizal networks in the soil or the plants' rhizosphere.

There is alternative electrochemical impedance method to measure static electrical parameters, such as resistance and capacitance, at high frequency alternative currents (AC). However, different electrochemical circuits can have the same electrochemical impedance. The description of equivalent electrical circuits based on electrochemical impedance AC measurements is based on the researcher's intuition and can lead to various mistakes [29]. Moreover, this method cannot characterize dynamic changes and non-linear events, such as ion channel opening and closing.

The propagation of passive electrical signals in nerves [28,30] and plants [19] is usually interpreted in terms of the cable model. The cable theory of the flow of electricity in a leaky cable was created by Lord Kelvin, who derived the equations to study the transatlantic telegraph cable. Hodgkin and Rushton [28] and Rall [30] applied the cable theory to passive electrical flow in membrane cylinders and neurons.

Figures 8,10,12 demonstrate a good match with the results of the experiment presented in Figures 2–4. The information gained from this mathematical modeling and analytical study of electrotonic signal transduction between *Aloe vera* plants using underground pathways in soil can be used not only to elucidate the effects of electrostimulation on higher plants coupled through the soil but also to observe and predict these effects not only experimentally but also via simulations that is faster and cheaper.

5. Conclusion

The pulse train, sinusoidal and a triangular saw-shape voltage profiles can be used for electrostimulation of plants and fast underground electrotonic signal transmission between plants. Electrical voltage from a function generator $V_{in}(t)$ applied to Pt-electrodes inserted into a leaf is converted due to electrical cell-to-cell coupling between cells in plant tissue by an electrical differentiator. The amplitude and sign of electrotonic potentials in both electrostimulated and neighboring *Aloe vera* plants depend on the amplitude, rise and fall of the applied voltage. Electrostimulation by a sinusoidal wave from a function generator induces electrical response in leaves with a phase shift. If voltage gated ion channels are closed and not involved in signal transduction along a plasma membrane, the propagation of passive electrotonic potentials can be described by a cable theory along a circuit consisting of plasma membrane capacitors C_1 and resistors R_1 and resistance along a plasma membrane R_2. Electrical circuits in the roots and at the root/soil interface are very complicated and many authors proposed different active and passive equivalent electrical schemes [31–36]. Due to additional RC-circuits in a root and soil, the duration of electrotonic potentials can increase. Electrical signals induced by electrostimulation of a leaf of one plant can be transmitted not only to the roots of the same plant but even to the leaves of a neighboring plant. More accurate mathematical models that take into account nonlinear effects will be explored.

Acknowledgement

This article is based on work supported in part by the National Science Foundation under Grant No. 1655280 and in part by the National Institute of Health under Grant No. 1R25GM106994-01.

Conflict of Interest

All authors declare no conflict of interest in this paper.

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