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Electrical signal transmission in the plant-wide web

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ABSTRACT

Plants can communicate with other plants using wireless pathways in the plant-wide web. Some examples of these communication pathways are: (1) volatile organic compounds' emission and sensing; (2) mycorrhizal networks in the soil; (3) the plants' rhizosphere; (4) naturally grafting of roots of the same species; (5) electrostatic or electromagnetic interactions; and (6) acoustic communication. There is an additional pathway for electrical signal transmission between plants - electrical signal transmission between roots through the soil. To avoid the possibility of communication between plants using mechanisms (1)–(6), soils in pots with plants were connected by Ag/AgCl or platinum wires. Electrostimulation of *Aloe vera*, tomato, or cabbage plants induces electrotonic potentials transmission in the electro-stimulated plants as well as the plants located in different pots regardless if plants are the same or different types. The amplitude and sign of electrotonic potentials in electrostimulated and neighboring plants depend on the amplitude, rise, and fall of the applied voltage. Experimental results displayed cell-to-cell electrical coupling and the existence of electrical differentiators in plants. Electrostimulation by a sinusoidal wave induces an electrical response with a phase shift. Electrostimulation serves as an important tool for the evaluation of mechanisms of communication in the plant-wide web.

1. Introduction

Plants communicate using different pathways [1–8]: (1) volatile organic compounds' emission and sensing [1,9,10]; (2) mycorrhizal networks in the soil [11–13]; (3) the plants' rhizosphere (root ball) [12]; (4) naturally grafting of roots of the same species [14]; (5) electrostatic or electromagnetic interactions [15–18]; (6) acoustic communication [19]. Recently we found that there is an additional pathway for electrical signal transmission between neighboring plants - fast underground electrical signal propagation between roots through the soil [3,7,16]. The possibility of electrical communication between plants in different pots connected by a metal conductor to avoid the signal transduction between two plants in the same pot through mycorrhizal networks in the soil will be interesting to pursue.

Electrostimulation of plants can induce activation of ion channels and ion transport [5,20–25], gene expression [26,27], enzymatic systems activation [28], electrical signaling [5], plant movements [29,30], enhance wound healing, repair plant-cell damage, and influence plant growth [23]. The electrostimulation by bipolar sinusoidal or triangular periodic waves induce electrical responses in plants, fruits, roots and seeds with fingerprints of generic memristors [30]. Herde et al. [26] found that electrical current application (10 V, 30 s) activates *pin2* gene expression in tomato plants and increases endogenous levels of abscisic acid.

In small neurons, exponentially decreasing electrical potentials are referred to as electrotonic potentials [31,32]. Electrotonic potentials exist not only in small neurons but also in plants [5,7,24,25]. Electrostimulation of electrical circuits in the Venus flytrap, *Aloe vera*, *Arabidopsis thaliana, Mimosa pudica*, apple fruits, and potato tubers induce electrotonic potentials with amplitude exponentially decreasing along vascular bundles [5]. In the electrical stimulation of the Venus flytrap, the lower leaf induces electrotonic signals within the entire plant. The trap closes if the stimulating voltage of the lower leaf is above the threshold level of 4.4 V [24]. Electrotonic potentials can induce action potentials in plants [24], small neurons, and dendrites [32].

Using the synchronous electrostimulation of plants from two different points, collision of propagating electrotonic potentials between them was found [5]. These electrical potentials can propagate with either a positive or negative pole in front of them. If a signal with a positive front collides with a negative one, they will amplify each other. However, if two electrical signals with positive fronts collide, they will partially annihilate each other.

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

Abbreviations: C, capacitance; *PFA*, perfluoroalkoxy alkane polymer; *R*, resistance; *V*, voltage; V_{in}, input voltage; λ, the length of electrotonic potential..

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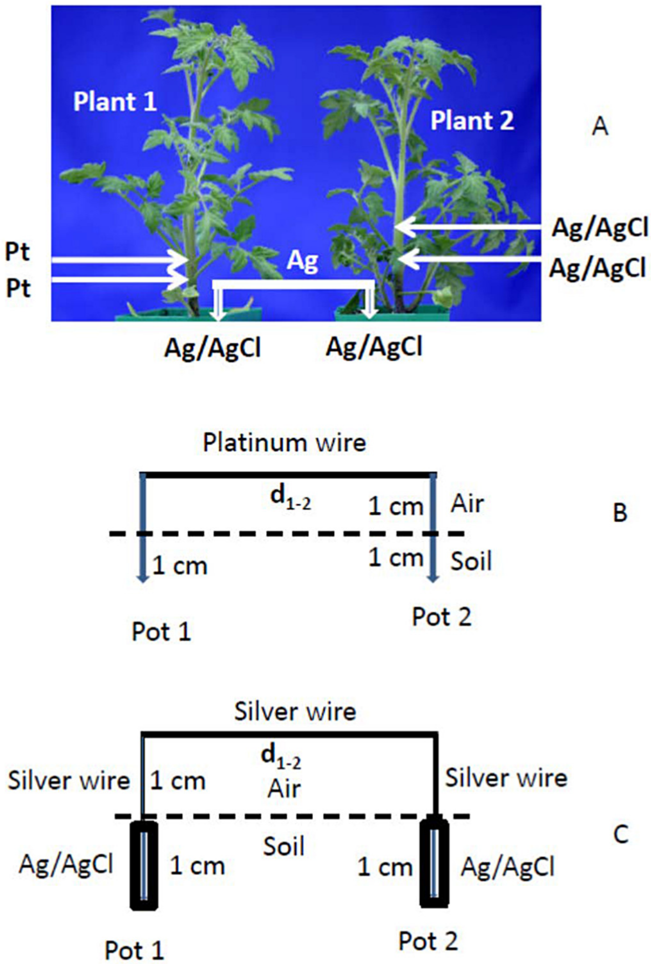


Scheme 1. Electrical connections between two plants in different pots (A); connection by platinum wire (B) or by double ended Ag/AgCl electrode (C). The length of a metal wire connection above the two pots is d_{1-2}.

during the day. CO_2 acquired by *Aloe vera* at night is temporarily stored as malic and other organic acids, and is decarboxylated the following day to provide CO_2 for fixation in the Benson-Calvin cycle behind closed stomata. Electron microscopy shows two distinct parts of the *Aloe vera* L. leaf: outer green rind and inner clear pulp, with vascular bundles located in the pulp and adjacent to the green rind.

Tomato and cabbage plants are dicotyledons and their stomata are open during the day and closed at night.

Plants can detect their neighbor also at the root level [33]. Soil is a good electrical conductor for transmission of electrical signals between plants [3,7,16,34,35]. The goal of this work is to find if fast electrical signal conduction exists between neighboring plants in separate pots connected by electrical conductors without volatile organic compounds' emission, mycorrhizal networks in the soil, roots grafting, or acoustic communication.

2. Materials and methods

2.1. Plants

Fifty tomato (*Lycopersicon esculentum* Mill. cv Cosmonaut Volkov) plants were grown in plastic pots with sterilized potting soil in a plant growth chamber (*Environmental Corporation*). The soil around the tomato plants was treated with water every day. All measurements were performed on 21-to 28-day-old tomato plants.

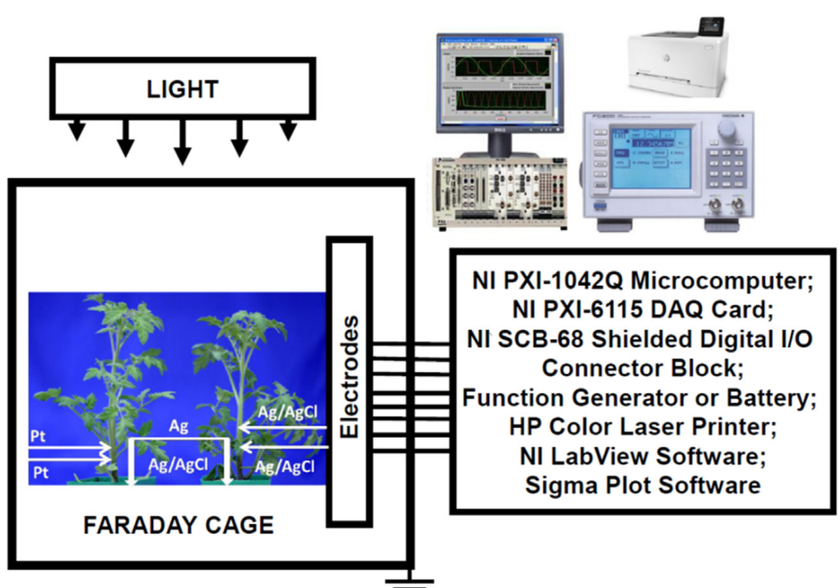
Fifty *Aloe vera* L. plants with 20–35 cm leaves were grown in clay pots with sterilized potting soil.

Seedlings of Bonnie Best Cabbage (*Brassica oleracea* L.) were purchased from Bonnie Plant Farm (Union Spring, Alabama).

All experiments were performed on healthy adult specimens. The volume of the soil was 1.0 L. Plants were exposed to a 12:12 h light/dark photoperiod at 22 °C. The average air humidity was 40% and the irradiance was 550–800 μmol photons m^{-2} s^{-1} PAR at plant level.

2.2. Electrodes

All measurements were conducted in the laboratory at 21 °C inside a Faraday cage mounted on a vibration-stabilized table. PFA (Perfluoroalkoxy Alkane Polymer) 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 tips without PFA 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



Scheme 2. Experimental setup. Function generator or 1.5 V battery connected to platinum electrodes were used for electrostimulation of plants.

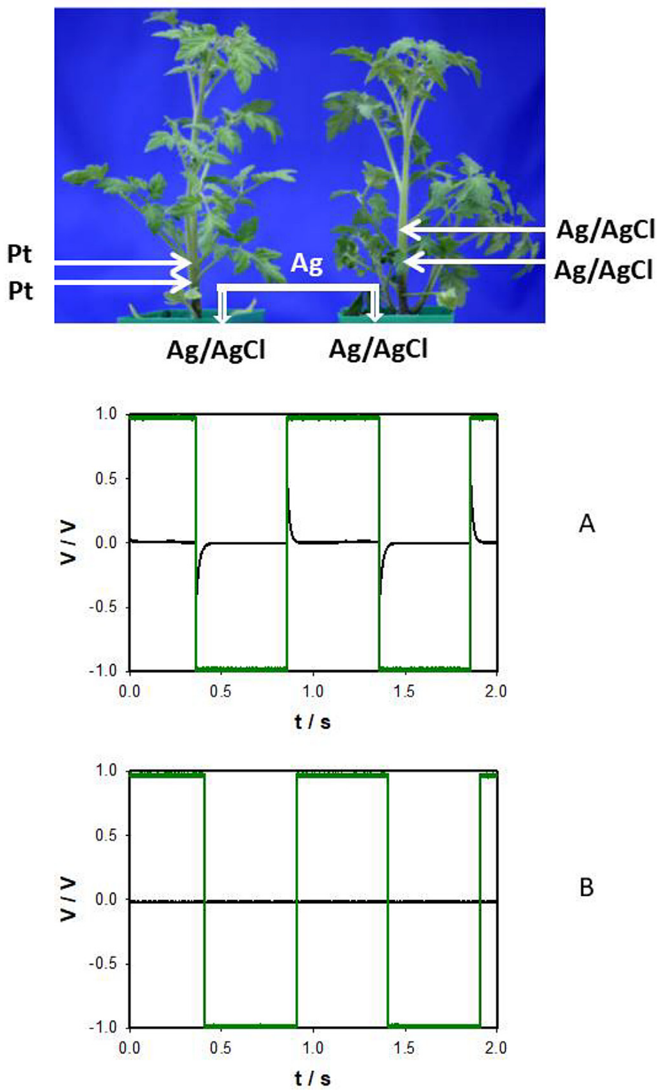


Fig. 1. Potential difference V between Ag/AgCl electrodes inserted to the tomato stem along vascular bundles (black lines) was induced by ± 1 V pulse train with 1 Hz frequency from function generator (green lines), which was connected to Pt-electrodes in the stem of another tomato plant. Distance between Pt electrodes was 0.2 cm. Measurements were performed at 200,000 scans/s with low pass filter at 100,000 scans/s. Two pots were connected by the double ended Ag/AgCl electrode with $d_{1-2} = 23$ cm (A) or without connection between pots (B). Distance between lower Pt electrode or Ag/AgCl and soil was 3 cm. Distance between Ag/AgCl electrodes was 1.5 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

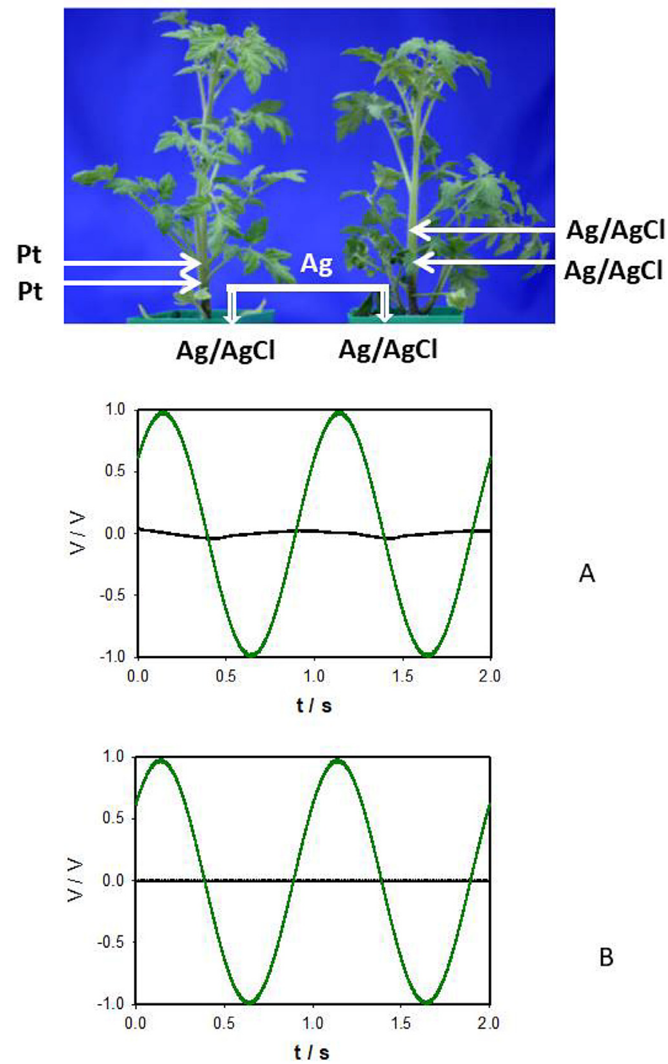


Fig. 2. Potential difference V between Ag/AgCl electrodes inserted to the tomato stem along vascular bundles (black lines) was induced by ± 1 V sinusoidal waive with 1 Hz frequency from function generator (green lines), which was connected to Pt-electrodes in the stem of another tomato plant. Distance between Pt electrodes was 0.2 cm. Measurements were performed at 200,000 scans/s with low pass filter at 100,000 scans/s. Two pots were connected by the double ended Ag/AgCl electrode with $d_{1-2} = 23$ cm (A) or without connection between pots (B). Distance between lower Pt electrode and soil was 2.5 cm. Distance between lower Pt electrode or Ag/AgCl and soil was 3 cm. Distance between Ag/AgCl electrodes was 1.5 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of the anode's surface. Stabilization of the electrodes was accomplished by placing two Ag/AgCl electrodes in a 0.1 M KCl solution for 24 h 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 the plants.

Platinum electrodes were prepared from PFA-coated platinum wires (99.99% purity; *A-M Systems, Inc., Sequim, WA, USA*) with a diameter of 0.076 mm. Platinum electrodes are stable over a wide range of potentials, in acidic and alkaline solutions, and in the presence of redox components.

We allowed the plants to rest for 2 h after electrode insertion. Electrodes were placed along the vascular bundles of a stem and also in soil in some control experiments.

To avoid root-to-root connections or mycorrhizal networks between plants, we connected pots with tomato or *Aloe vera* plants by a metal wire (Scheme 1). Two types of wires (platinum or Ag/AgCl) covered by PFA (*A-M Systems, Inc., Sequim, WA, USA*) were used. Both of the ends of a silver wire were covered by electrodeposition of AgCl on 10 mm long wire tips without PFA coating. Platinum connecting electrodes were prepared from PFA coated platinum wires (99.99% purity; *A-M Systems, Inc., Sequim, WA, USA*) with a diameter of 0.076 mm.

2.3. Data acquisition

Experimental setup is shown in Scheme 2. 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 electrodes. The system integrated standard low-pass anti-aliasing filters at one half of the sampling frequency.

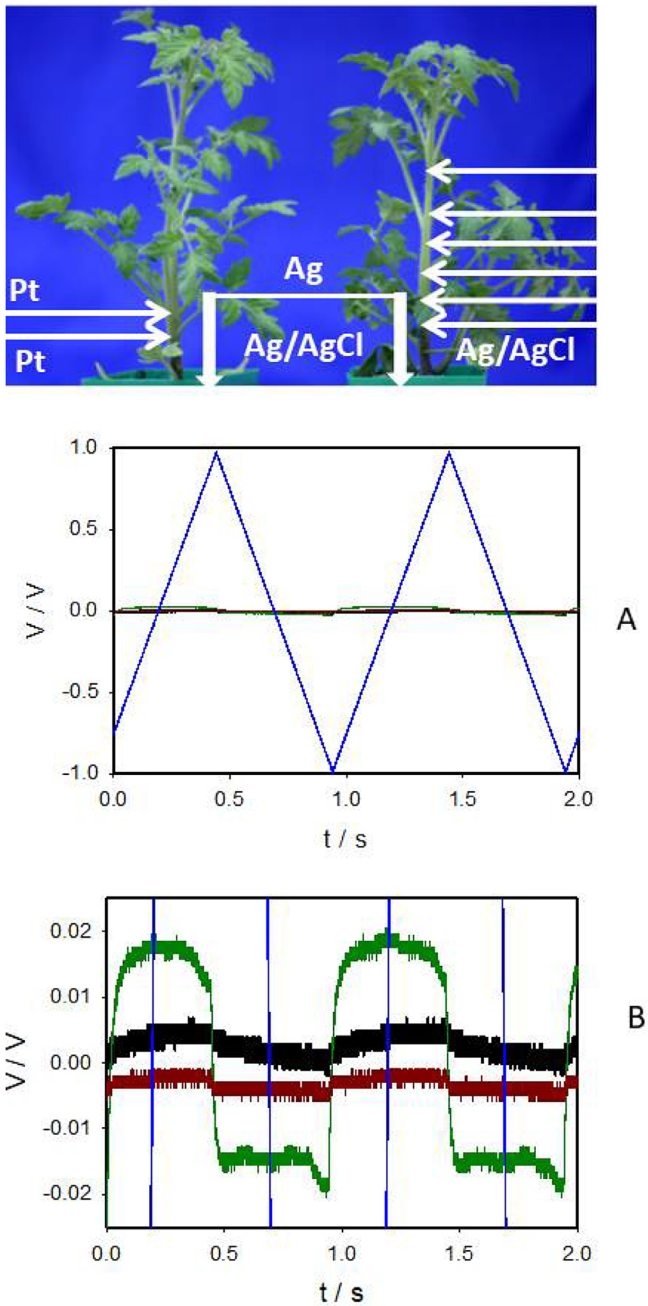


Fig. 3. Potential difference *V* between Ag/AgCl electrodes inserted to the tomato stem along vascular bundles (green, black and red lines at different distances) was induced by ±1 V triangular saw-shape voltage with 1 Hz frequency from function generator (blue lines), which was connected to Pt-electrodes in the stem of another tomato plant. Distance between Pt electrodes was 0.2 cm. Measurements were performed at 200,000 scans/s with low pass filter at 100,000 scans/s. Two pots were connected by the double ended Ag/AgCl electrode with d_{1-2} = 23 cm. Panel B was extracted from panel A to show high resolution electrical responses. Distance between lower Pt electrode and soil was 2.5 cm. Distance between lower Pt electrode or Ag/AgCl and soil was 3 cm. Distance between Ag/AgCl electrodes was 1.5 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.4. Electrostimulation

Two methods of plant electrostimulation were used: the function generator and the 1.5 V batteries. The function generator FG300 (*Yokagawa, Japan*) was interfaced to the NI-PXI-1042Q microcomputer (*National Instruments, Austin, TX, USA*) and used for the electrostimulation of plants (Scheme 2). The function generator provides many options for

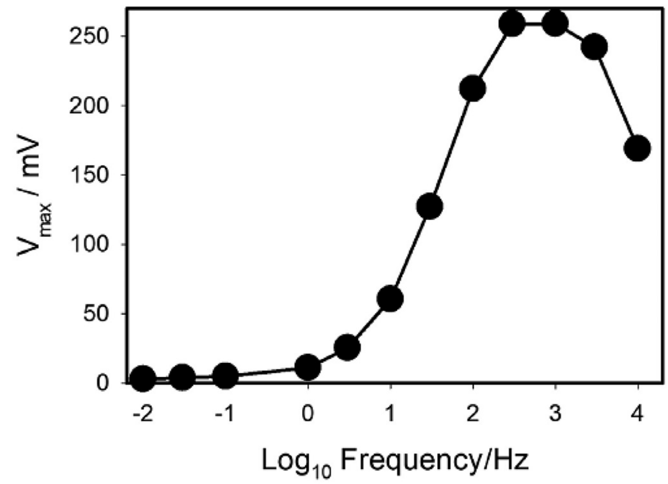


Fig. 4. Amplitude – frequency characteristics of electrical responses *V* between Ag/AgCl electrodes inserted to the tomato stem along vascular bundles induced by sinusoidal electrical wave with voltage varies from −1.5 V and 1.5 V from function generator, which was connected to Pt-electrodes inserted to a neighboring tomato plant. Distance between Pt-electrodes was 0.2 cm and distance between Ag/AgCl electrodes was 2 cm. Both pots with plants located on 10 cm distance were connected by a silver wire covered by PFA. Both of the ends without PFA coating of a silver wire were covered by electrodeposition of AgCl.

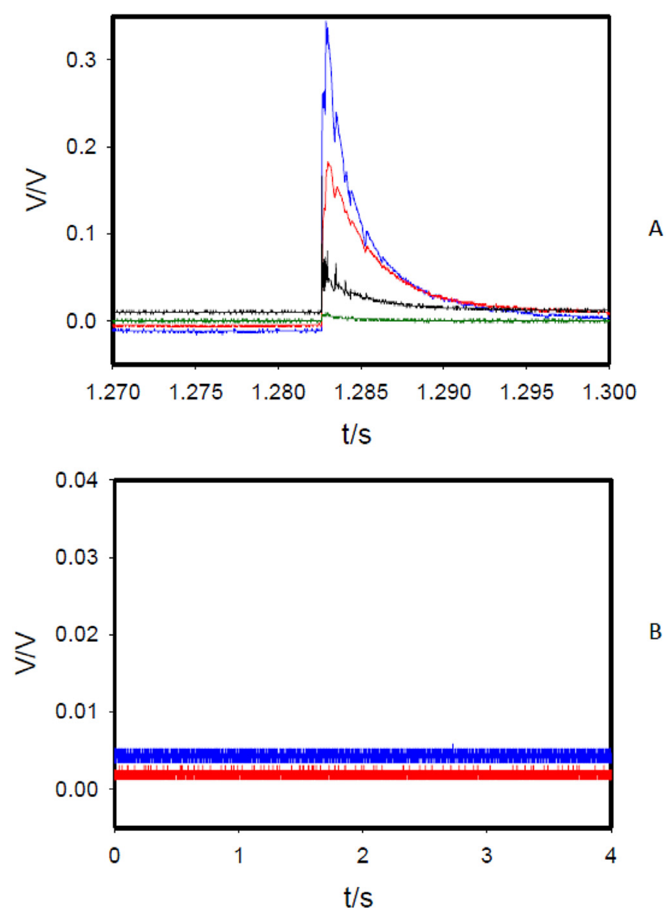


Fig. 5. Electrical responses between Ag/AgCl electrodes in tomato stem induced by 1.5 V electrical battery which was connected to Pt-electrodes inserted to a neighboring tomato plant. Distance between Pt-electrodes was 0.2 cm and distance between Ag/AgCl electrodes was 2 cm. Both pots with plants located on 10 cm distance were connected by a silver wire covered by PFA (A) or not connected by any conductors (B). Both of the ends of a silver wire were covered by electrodeposition of AgCl on d_{1-2} = 10 mm long wire tips without PFA coating.

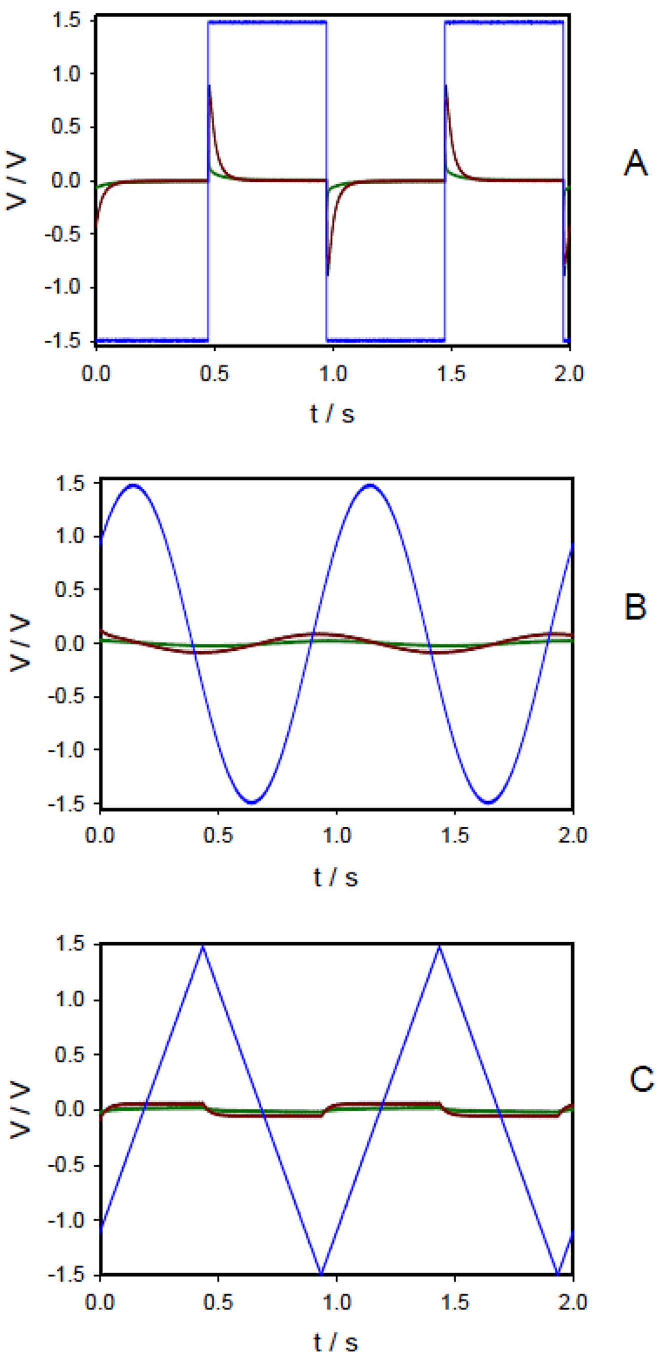


Fig. 6. Potential difference *V* between Ag/AgCl electrodes inserted to *Aloe vera* leaf along vascular bundles was induced by ±1.5 V pulse train (A), sinusoidal (B) or triangular saw-shape (C) waive with 1 Hz frequency from function generator (blue lines), which was connected to Pt-electrodes in a leaf of another *Aloe vera* plant. Distance between Pt electrodes was 0.4 cm. Measurements were performed at 100,000 scans/s with low pass filter at 50,000 scans/s. Two pots were connected by the double ended Ag/AgCl electrode with d_{1-2} = 10 cm. Distance between lower Pt electrodes was 2 mm. Distance between Ag/AgCl electrodes was 2 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the electrostimulation, such as shape, duration, and frequency of stimulation.

2.5. Images

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

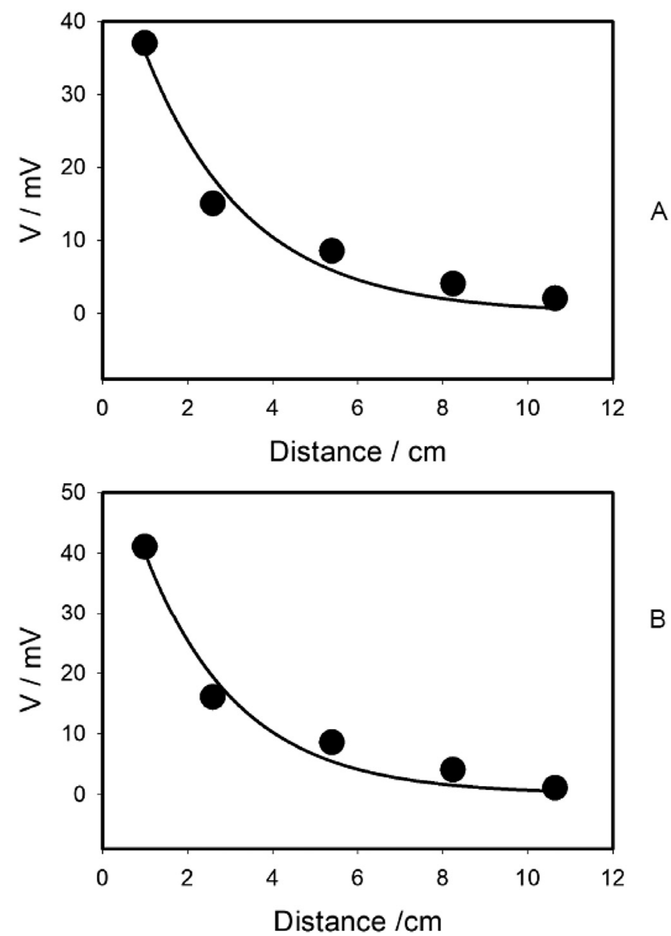


Fig. 7. Dependencies of amplitude of electrotonic potentials on distance between Ag/AgCl electrodes inserted along vascular bundles in *Aloe vera* leaf induced by sinusoidal (A) or triangular saw-shape voltage (B) from a function generator connected to platinum electrodes in a neighboring *Aloe vera* plant. Distance between Pt-electrodes was 0.2 cm and distance between Ag/AgCl electrodes was 2 cm. Both pots with plants located on 10 cm distance were connected by a silver wire covered by PFA. Both of the ends of a silver wire were covered by electrodeposition of AgCl on d_{1-2} = 10 mm long wire tips without PFA covering. Measurements were performed at 100,000 scans/s with low pass filter at 50,000 scans/s.

2.6. Statistics

All experimental results were reproduced at least 16 times using different plants. Software SigmaPlot 12 (*Systat Software, Inc., San Jose, CA, USA*) was used for statistical analysis of experimental data.

3. Results

Electrostimulation of a plant by a square pulse from a function generator induces percussive electrical signals along the same plant and in other plants in the same pot. Soil can work as an electrical conductor between roots of plants. To avoid root-to-root connections or mycorrhizal networks between plants, we connected soil near plants in different pots by a platinum or silver wire. Since soil and plants have electrolyte solution with Cl^- anions, we also used double sided Ag/AgCl electrode (Scheme 1). The pulse train (Fig. 1), sinusoidal (Fig. 2) and a triangular saw-shape (Fig. 3) voltage profiles were used for electrostimulation.

Amplitude of electrotonic potentials increases to a maximum amplitude with increasing applied voltage frequency, and decreases at high frequencies (Fig. 4) as it was estimated and predicted in our theoretical model of electrical circuits in plants [16].

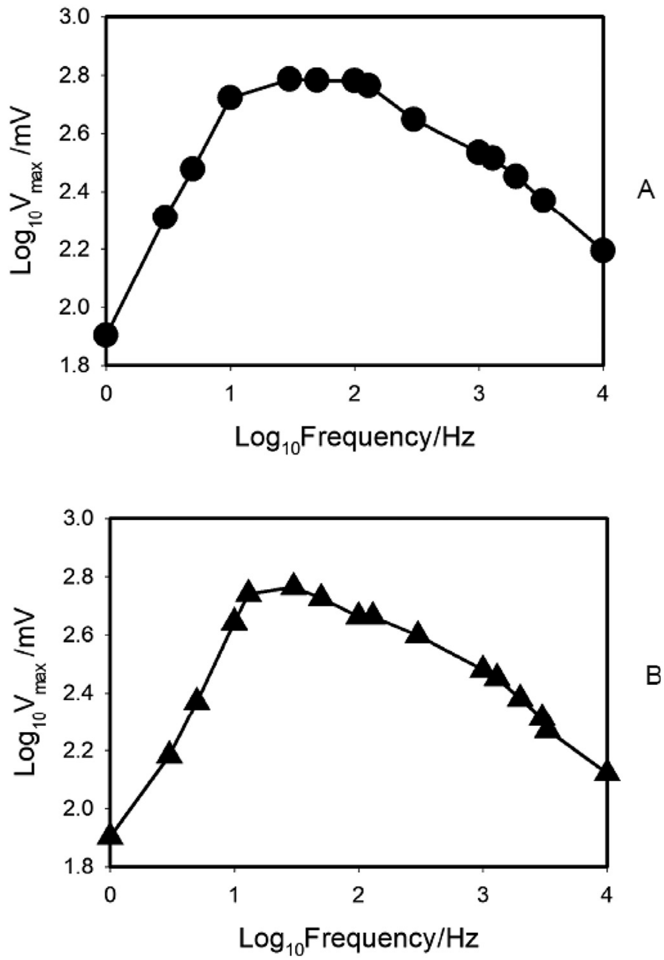


Fig. 8. Amplitude – frequency characteristics of electrical responses V between Ag/AgCl electrodes inserted to the *Aloe vera* leaf along vascular bundles induced by sinusoidal (A) or triangular saw-shape (B) electrical wave with voltage varies from −1.5 V and 1.5 V from function generator, which was connected to Pt-electrodes inserted to a neighboring *Aloe vera* plant. Distance between Pt-electrodes was 0.2 cm and distance between Ag/AgCl electrodes was 2 cm. Both pots with plants located on 10 cm distance were connected by a silver wire covered by PFA. Both of the ends of a silver wire were covered by electrodeposition of AgCl on $d_{1-2} = 10$ mm long wire tips without PFA coating.

Fig. 5B shows that there is no electrotonic signal transmission between plants in the absence of electrical conductors between soils or plants in both pots. It means that fast electrotonic signal transmission between neighboring plants is not caused by volatile organic compounds' emission, mycorrhizal networks in the soil, the plants' rhizosphere, naturally grafting of roots, electrostatic or electromagnetic interactions, and acoustic communication.

If both tomato plants are substituted by *Aloe vera* plants, results on electrostimulation and transmission of electrical signals look very similar (see Figs. 1, 2, 3 and 6).

Amplitude of electrotonic potentials decreases exponentially with distance (Fig. 7):

$$V = a\mathrm{Exp}(-\mathrm{Distance}/\lambda) \quad (1)$$

with $\lambda = 2.44$ cm (Mean 2.44 cm, Median 2.44 cm, Std. Dev. 0.05 cm, Std. Err. 0.015 cm,

99% Conf. 0.05 cm, $n = 10$). Therefore, the constant of length λ, which indicates how far an electrical signal will spread in the leaf of the *Aloe vera*, is $\lambda = 2.44$ cm. The constant of length of electrotonic potential transmission in tomato plant is $\lambda = 4.80$ cm (Mean 4.80 cm, Median 4.80 cm, Std. Dev. 0.11 cm, Std. Err. 0.03 cm, 99% Conf. 0.11 cm, n = 10). λ is the distance from the point at which voltage is injected to the point at which the electrotonic depolarization has fallen to e^{-1}, i.e. 0.37, of its original value (V_{in}).

Amplitude of electrotonic potential depends on frequency of sinusoidal waive applied for electrostimulation of an *Aloe vera* (Fig. 8). Amplitude of electrotonic potentials increases to a maximum amplitude with increasing of applied voltage frequency, and decreases at high frequencies as it was estimated by Volkov and Shtessel [16].

If one of the *Aloe vera* plants is substituted by tomato or cabbage plants, results on electrostimulation and transmission of electrical signals look very similar (Fig. 9).

Wet soil is a good electrical conductor [35]. A function generator can be used to stimulate soil and produce a pulse train, sinusoidal and a triangular saw-shape voltage profiles. A function generator connected to platinum electrodes induces propagation of sinusoidal electrical waves without a phase shift between bowls of soil connected by a platinum wire (Fig. 10). Amplitude of electrical waves depends on distance between electrodes and soil resistance between them. Soil resistivity depends on moisture, chemical composition, temperature, cation exchange capacity, salinity, texture, and pH. Soil electrical conductivity is usually measured by the four-electrode method [35]. Two transmitting electrodes electrostimulate soil and two receiving electrodes measure electrical response in the soil. There is no electrical response between the Ag/AgCl electrodes if both bowls are not connected by a metal conductor.

4. Discussion

There are different possibilities for communication within and between plants such as cell-to-cell, root-to-root, shoot-to-shoot, and between roots and shoots [3–5,7,16,24,25,30,35–40].

Shtessel [16] created a theory which described with very high accuracy experimental data on signal transmission inside a single plant and between two identical plants through soil. There are a few different pathways for underground signal transmission through soil: (1) mycorrhizal networks in the soil; (2) the plants' rhizosphere; (3) naturally grafting of roots of the same species; (4) and direct electrical signal transmission through soil which is a very good electrical conductor. In our present paper, we eliminated pathways (1)–(3) and studied electrical signal transduction (4) between multiple plants. For simplicity, we consider in the present work electrical signal transmission between 2 plants. We have similar results in a network of a few plants connected by electrical conductors.

Usually, neurobiologists and electrophysiologists measure action and electrotonic potentials as an open-circuit voltage, which is a difference between two terminals of a device when disconnected from electrical circuit. This non-invasive method exploits voltmeters with very high input impedance. For electrostimulation, we used the pulse train, sinusoidal and a triangular saw-shape voltage profiles. The amplitude and sign of passive electrotonic potentials depend on the amplitude, rise and fall of the applied voltage (Figs. 1-3, 5, 6, 9). Electrostimulation by a sinusoidal wave from a function generator induces electrical response between inserted Ag/AgCl electrodes with a phase shift of 90° at low frequencies of electrostimulation (Fig. 2). The phase shift decreases at high frequencies of electrostimulation. This phenomenon shows that electrical networks in plants have electrical differentiators in cell-to-cell coupling. Electrical differentiators were found in *Arabidopsis thaliana*, *Aloe vera*, *Mimosa pudica*, tomato plants, and in the Venus flytrap [3, 5, 16, 24. 30]. Cell-to-cell coupling in plants is well supported in previous literature [3,5,16,36–41].

The sign of an electrotonic response depends on the polarity of electrostimulating electrodes and the amplitude of electrotonic potentials depends the on amplitude of applied voltage. The response does not obey the "all-or-none rule". It is not an action potential but rather corresponds to the propagating electrotonic potential [42].

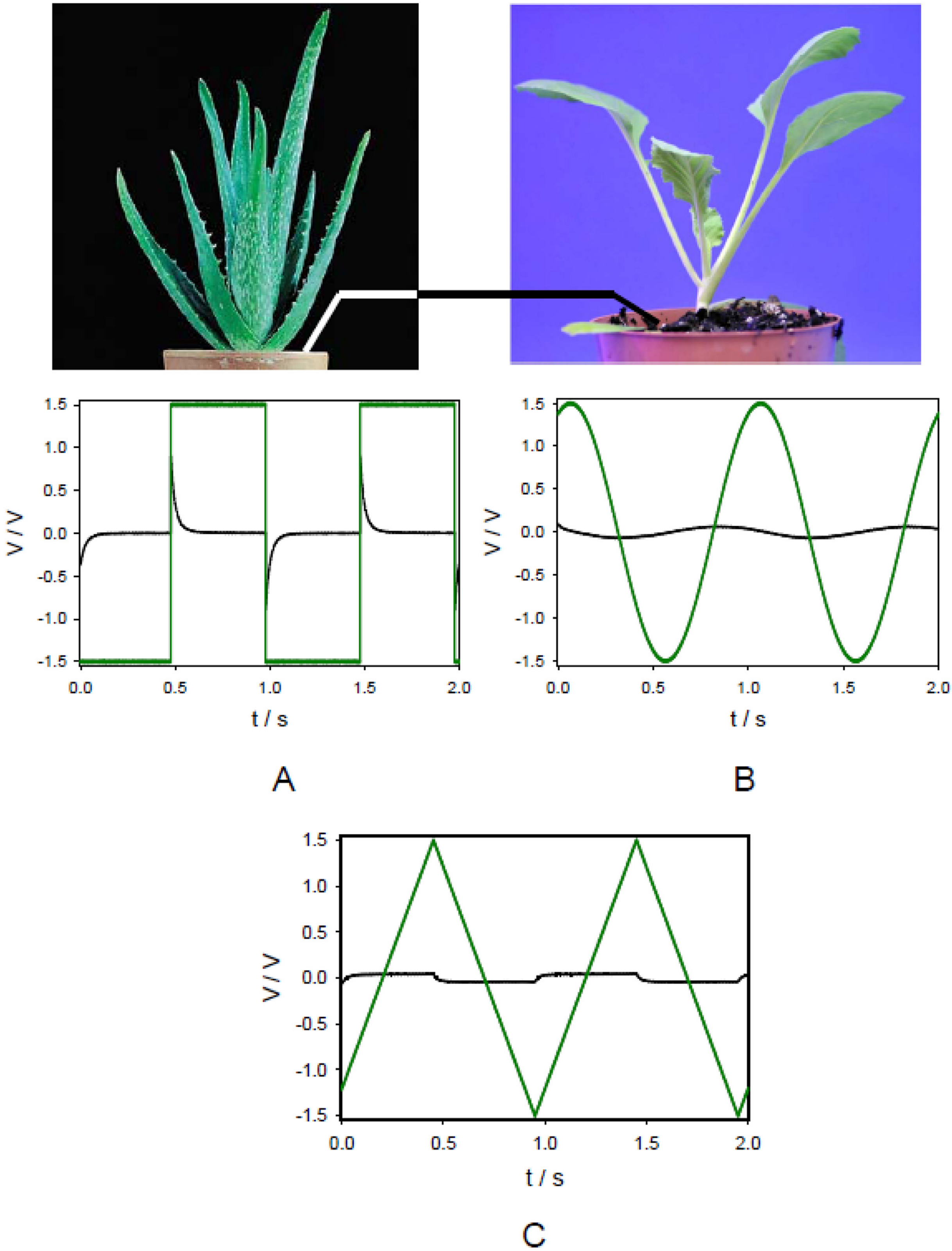


Fig. 9. Potential difference *V* between Ag/AgCl electrodes inserted to a cabbage stem along vascular bundles (black lines) was induced by ±1.5 V pulse train (A), sinusoidal (B) or triangular electrical waives with 1 Hz frequency from function generator (green lines), which was connected to Pt-electrodes in a leaf of *Aloe vera* plant. Distance between Pt electrodes was 0.4 cm. Measurements were performed at 100,000 scans/s with low pass filter at 50,000 scans/s. Two pots were connected by the double ended Ag/AgCl electrode with $d_{1-2} = 10$ cm. Distance between Ag/AgCl electrodes was 1.5 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

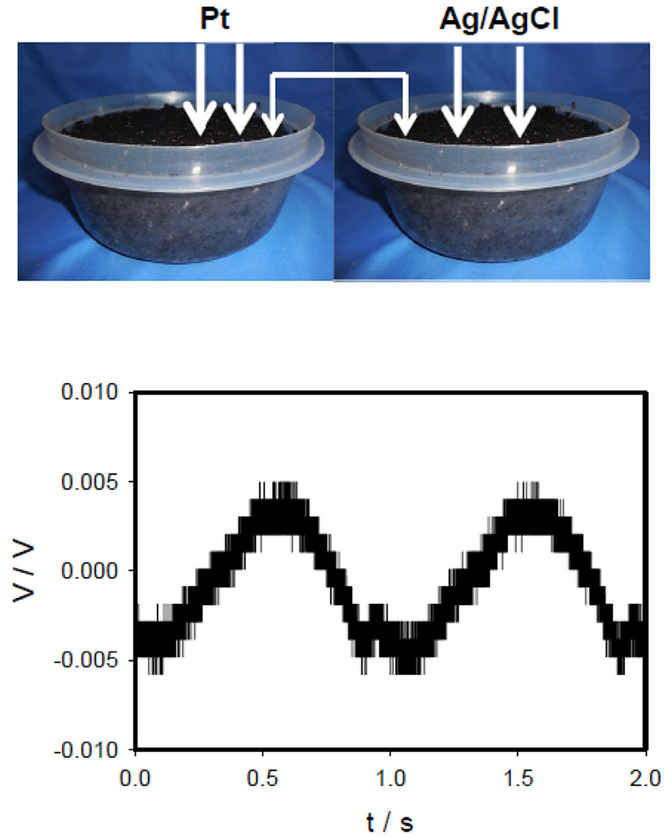


Fig. 10. Electrostimulation of soil by a ± 1.5 V sinusoidal wave from a function generator connected to platinum electrodes immersed to soil. Measurements of electrical responses of Ag/AgCl electrodes were performed at 50,000 scans/s with low pass filter at 25,000 scans/s. Distance between Pt electrodes was 2 cm, distance between Ag/AgCl electrodes was 3 cm.

The reaction of the plant strongly depends on the shape of electrical stimulus. 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:

$$V(t) = RC\frac{d}{dt}(V_{in}(t) - V(t)) \quad (2)$$

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

If

$$\frac{dV(t)}{dt} \ll \frac{dV_{in}(t)}{dt}, \quad (3)$$

Then

$$V(t) = RC\frac{d}{dt}V_{in}(t). \quad (4)$$

According to Eq. (4).

$$V_{in} = A\ \sin(\omega t) \quad (5)$$

yields.

$$V(t) = \omega RCA\ \cos(t) \quad (6)$$

i.e. the 90° phase shift is expected. The amplitude of $V(t)$ increases with increasing the stimulating frequency of scanning at low frequencies according to eq. 4, but decreases at very high frequencies as it has presented in Figs. 4 and 8.

The pulse train and sinusoidal electrical waives illustrate the differentiation capabilities of plants; the sinusoidal voltage demonstrates the phase shift in the voltage propagation. The triangular voltage wave can demonstrate how the time-varying voltage with a constant slope propagates through the leaf. The transformation of such time-varying signal to a constant one is expected due to a possible differential property of a plant. The amplitude and sign of electrotonic potentials depend on the shape, rise and fall of the applied voltage during electrostimulation, and the distance from electrostimulating electrodes, amplitude and polarity of the applied voltage (Figs. 1-3, 5, 6, 9). These electrical responses are not action potentials since their amplitude and polarity depend on the applied voltage (Figs. 1-3, 5, 6, 9).

Adamatzky [43] studied a possibility of making electrical wires from plants and found that lettuce seedlings act as a potential divider. Stavrinidou et al. [44] manufactured analog and digital organic electrotonic circuits in vascular bundles of *R. floribunda*. Electrical diagnostics of plants gives information about plant health and possible diseases and infections [45,46]. The equivalent electrical circuit of generation, transmission and recording of electrotonic potentials between plants in different pots introduced by Volkov and Shtessel [16] can be extrapolated to electrical signal transmission in the plant-wide web.

5. Conclusions

There are different electrical, chemical and electrochemical pathways for signaling within and between plants. Electrical signal transmission is fast in comparison with chemical signaling which is controlled by a slow diffusion. Electrostimulation of *Aloe vera*, tomato, or cabbage plants induces electrotonic potentials transmission in the electro-stimulated plants as well as the neighboring plants located in different pots regardless if plants are the same or different types. Experimental results displayed cell-to-cell electrical coupling and the existence of electrical differentiators in plants. Electrostimulation serves as an important tool for the evaluation of mechanisms of communication in the plant-wide web.

Disclosure of potential conflicts of interest

The author declares no competing financial interest.

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Conflict of interest

The authors declare no conflict of interest in this paper.

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