



# Electrical signals as an option of communication with plants: a review

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**Abstract** As plants are living forms that cannot communicate their condition (stress, requirements) as animals, they have been studied to find chemical or physical signals that could help understand the plant requirements for several purposes such as substances and food production. Different research supports electrical signals (ES) related to different stress conditions in plants as damage or drought. Some others have identified and classified these signals generated by stress condition using diverse Artificial intelligence (AI) techniques. Finally, some other researches have used electricity as a stimulator obtaining a response as chemical compounds production, gene expression and growth-promoting. In a few words, ES from plants can be interpreted, which could also be sent back to plants. Based on the bibliographic revision in this work, it is proposed that experiments and research, where the ES serves to activate chemical and physiological mechanisms or as elicitor, are

required to consider the electrical signals as a possible communication pathway with plants.

**Keywords** Electricity · Physiological · Communication · Message · Elicitor · Stress

## 1 Introduction

Nowadays, researchers can get information from the plant, but also deliver a message to cause a change, for example, gibberellins are a phytohormone that the plant naturally produces, and it is related to dormancy breaking in seeds; if this substance is applied exogenously to seeds, they will break dormancy and germinate (Cerabolini et al. 2004; Hedden 2019). The presence of phytohormones and other substances can help to determine the plant condition; nevertheless, the process to know if this substance is presented will require the realization of experiments in the laboratory, such as mass spectrometry (Delatorre et al. 2017; Wang et al. 2017; Simura et al. 2018) which requires a plant sample, the application of expensive reagents, special equipment and technicians prepared.

There are several possible information exchange channels, such as mycorrhizal webs and the general rhizosphere and roots relations; these channels were detected in an experiment where plants of *Vicia faba* were grown in association with *Rhizophagus*

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*irregularis*, a mycorrhizal fungus, and infested with aphids (*Acyrtosiphon pisum*). The neighbor plants that were not infested with aphids presented changes in volatiles compounds, as the infested ones, 24 h later (Babikova et al. 2013). Another possible communication channel is the release and caption of volatile organic compounds (VOC), as it was seen in an experiment where *Populus* tree leaves were scraped; all the plants, with and without damage, shared the same enclosure, and they had greater concentrations and rates of synthesis of phenolic compounds (Baldwin and Schultz 1983). Also, electromagnetic variations are seen as communication signals inside the plant (de Toledo et al. 2019). For example, when *Vicia faba* is burned or injured, a magnetic field occurs simultaneously with a long-distance signaling process; this signal provokes the synthesis of proteins that have importance in the insect predator defense (Bowles 1990). Finally, the soil can work as a conductive pathway for electrical signals (ES). It was demonstrated in an experiment where *Aloe vera* plants were electro-stimulated; the electrical signal was also sensed in neighbor plants (Volkov and Shtessel 2017). ES have physiological roles in helping to activate the leaf movement response in *Mimosa*, *Dionaea*, and *Drosera* (Sibaoka 1991; Opritov et al. 1991; Fromm and Lautner 2007; Gallé et al. 2015), pollination process in *Lilium*, *Hibiscus*, and *Incarvillea* (Dziubińska 2003), and Reactive Oxygen Species (ROS) production (Gilroy et al. 2016).

Other investigations evaluate methods to classify some kinds of ES using artificial intelligence (AI) and relate them to specific stress conditions to estimate or diagnose plant conditions (Chen et al. 2016; Li et al. 2016; Pereira et al. 2018). As summary, ES have been related to different types of stress and responses. Also, there are techniques to classify the signals and use them to know the plant condition in real-time; nevertheless, ES has never been reproduced and been applied to the plant. According to several authors, ES can be associated with a plant condition just as happen with phytohormones and other substances (Nadeem et al. 2016; Egamberdieva et al. 2017; Chhaya et al. 2020); thus, the application of ES related to specific stress or physiological process may induce a response in the plants better than applying ES arbitrarily. This work presents a revision of the literature where ES, related to some stress, are used to know the plant condition, and where ES is applied to plants to cause

positive effects; if the ES generate positive effects in plants, it is called that ES generates eustress in plants too. The manuscript principally shows types of stress-related to ES, the caption and classification techniques of ES measurement, and researches where electricity has been applied to obtain benefits in plants.

## 2 Electrical signals related to stress conditions

Several studies that reveal that plants generate different types of ES, being considered as the principals the Action potentials (APs), the Variation potentials (VPs), and the System potentials (SPs) (Sukhov et al. 2019c). The ES will depend on the kind of stimulus the plant is facing, like those listed in Table 1.

Different types of stimuli cause each kind of ES, but they have something in common. The APs are electrical signals that obey a frontier-cross shot. The intensity of the stimuli must exceed the frontier resistance value; when that occurs, the ES starts with a depolarization phase. The anion channels that depend on  $\text{Ca}^{2+}$  are activated when the concentration of that ion increases,  $\text{H}^+$ -ATPase is inactivated, and a flow of  $\text{Ca}^{2+}$  into the cell begins (Fig. 1a). The fast potential change inactivates the  $\text{Ca}^{2+}$  dependent channels. It activates the  $\text{K}^+$  channels, flowing out  $\text{K}^+$  anions, decreasing the  $\text{Ca}^{2+}$  concentration, and reactivating  $\text{H}^+$ -ATPase, starting with the repolarization phase (Fig. 1b) (Vodeneev et al. 2006; Felle and Zimmermann 2007). All that ion flux can be seen in a graphic as a voltage curve increase (depolarization) and a voltage curve decrease (repolarization) of the cell membrane (Fig. 1c). Once the signal is generated, it doesn't matter anymore if the stimuli' intensity increases or decreases (Sukhov 2016; Sukhova et al. 2017). There are three proposed propagation mechanism; the first is considered through the cytoplasm (symplastic pathway) the vascular tissue cells, specifically parenchyma (Opritov et al. 1991; Sukhov et al. 2011). The second proposes the propagation of the ES through the plant's sieve (Fromm and Lautner 2007; Zhao et al. 2015). The third combines the previous ones, the APs could be generated in parenchyma cells, and the sieve may work as an electrical pathway for the current (Sukhova et al. 2017).

The APs are generated by non-critical damage, a sensitive intervention that will affect plants but not in a catastrophic way (Sukhova et al. 2017; Szechynska-

**Table 1** Types of electrical signals that occur during specific damages or stimuli and the plant species

Damage or stimulus	Type of ES produced	Plant species	References
Electricity (DC and AC)	Action potential	<i>Chara corallina</i>	Krol et al. (2006)
		<i>Dionaea muscipula</i>	Bulychev and Krupenina (2010)
		<i>Nitellopsis obtusa</i>	Sevriukova et al. (2014)
		<i>Salix viminalis</i>	Kisnieriene et al. (2016, 2018)
		<i>Lycopersicon esculentum</i>	Fromm and Spanswick (1993)
		<i>Helianthus annuus</i> L.	Stankovic and Davies (1996)
			Stankovic et al. (1998)
Temperature decrease		Krupenina and Bulychev (2007)	
	Action potential	<i>Cucurbita pepo</i>	Retivin et al. (1997)
	System potential	<i>Zea mays</i>	Fromm and Bauer (1994), Opritov et al. (2005)
		<i>Dionaea muscipula</i>	Krol et al. (2006)
		<i>Populus trichocarpa</i>	Lautner et al. (2005)
Contact	Action potential	<i>Mimosa pudica</i>	Sibaoka (1991)
		<i>Dionaea muscipula</i>	Shepherd et al. (2008), Degli Agosti (2014)
		<i>Aldrovanda vesiculosa</i>	Krausko et al. (2017), Pavlovic et al. (2017)
		<i>Drosera capensis</i>	Williams and Pickard (1972a, b)
		<i>Chara corallina</i>	Fromm and Eschrich (1988a, b, c)
		<i>Arabidopsis thaliana</i>	
		<i>Drosera intermedia</i>	
Compounds (salt and amino acids)	Action potential	<i>Hordeum vulgare</i>	Felle and Zimmermann (2007)
Illumination changes	Action potential	<i>Dionaea muscipula</i>	Trebacz and Sievers (1998)
		<i>Anthoceros</i> sp.	Pikulenکو and Bulychev (2005)
Fire damage	Variation potential	<i>Nicotina tabacum</i> cv. <i>Samsun</i>	Hlaváčková et al. (2006)
	System potential	<i>Pelargonium zonale</i>	Sukhov et al. (2012)
		<i>Pisum sativum</i>	Sukhova et al. (2017)
		<i>Populus trichocarpa</i>	Lautner et al. (2005)
		<i>Lycopersicon esculentum</i>	Stankovic and Davies (1996)
		<i>Helianthus annuus</i> L	Stankovic et al. (1998)
		<i>Vicia faba</i>	Zimmermann and Felle (2009)
		<i>Glycine max</i>	Galle et al. (2013)
	<i>Cucurbita</i> sp.	Vodeneev et al. (2011)	
Temperature increase	Variation potential	<i>Pisum sativum</i>	Sukhov et al. (2014a, b)
	System potential	<i>Zea mays</i>	Sukhova et al. (2017)
			Vuralhan-Eckert et al. (2018)
Mechanical damage	Variation potential	<i>Pisum sativum</i>	Sukhova et al. (2017)
	System potential	<i>Vicia faba</i>	Zimmermann et al. (2009)
		<i>Hordeum vulgare</i>	Mousavi et al. (2013)
		<i>Arabidopsis thaliana</i>	
Different color of light	System potential	<i>Cucurbita pepo</i> L. var <i>medullosa</i>	Eschrich et al. (1988)

**Table 1** continued

Damage or stimulus	Type of ES produced	Plant species	References
Absciscic acid	System potential	<i>Salix viminalis</i>	Fromm et al. (1997)
Biotic stress	Action potential	<i>Hordeum vulgare</i>	Zimmermann et al. (2016)
(insect attack)	System potential	<i>Vicia faba</i> <i>Nicotiana tabacum</i>	
Re-watering	System potential	<i>Zea mays</i>	Vuralhan-Eckert et al. (2018)
	Action potential		Fromm and Fei (1998)

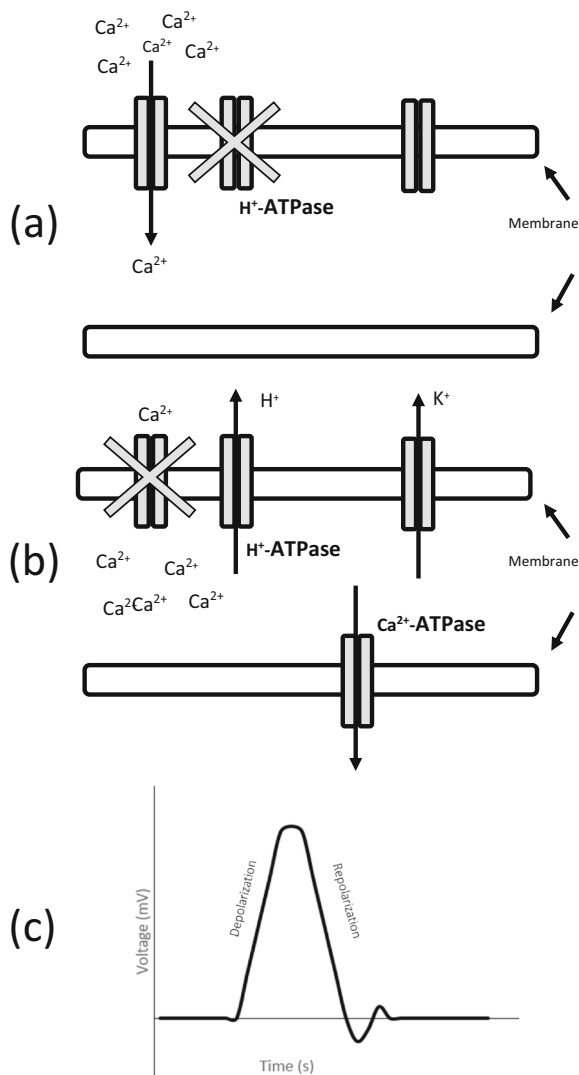
Hebda et al. 2017). The non-critical damage or stimuli can be listed in Table 1; these damages include the gradual decrease in temperature, as it happens at night, the application of a low electrical current, low changes in soil salinity, the physical interaction with some objects or animals (contact) and changes in light intensity (Pikulencko and Bulychev 2005; Krol et al. 2006; Felle and Zimmermann 2007; Krausko et al. 2017; Kiszneriene et al. 2018). On the other hand, the VPs are electrical signals that, unlike APs, will occur once the stimuli start; in this type, the amplitude of the signal will vary depending on the intensity and time exposure (Oprittov et al. 1991). The plant generates VPs signal once a damage occurs, and its generation mechanism has not been fully understood. It is proposed that could start with a hydraulic wave that travels through the xylem, also it is proposed that starts with a special substance that is produced after the plant suffers the damage, finally, is also proposed the combination of those two options, a hydraulic wave that travels through xylem and that carries a special damage-related substance. The activity mentioned induce the activation of mechano-sensitive  $\text{Ca}^{2+}$  channels or ligand-dependent  $\text{Ca}^{2+}$  channels, here starts the depolarization phase (Vodeneev et al. 2011, 2015; Sukhov et al. 2013; Katicheva et al. 2014, 2015). The increase in the concentration of  $\text{Ca}^{2+}$  could be considered the motive of the long-term inactivation of  $\text{H}^+$ -ATPase, driving in the long-term depolarization. The repolarization phase starts once the hydraulic or chemical signal ends and  $\text{Ca}^{2+}$  channels are inactivated and  $\text{H}^+$ -ATPase re-activated (Stahlberg et al. 2006; Fromm and Lautner 2007; Vodeneev et al. 2015; Sukhov 2016; Sukhova et al. 2017). The velocity of propagation and amplitude are inversely proportional to the distance traveled from the damage zone; it means that, as the signal propagates away from the damage zone, the amplitude and

velocity decrease (Vodeneev et al. 2012; Sukhov et al. 2013). The signal also is different. The VPs are characterized by an irregular depolarization; once the curve achieves the top value, the decrease of the voltage starts, the descent is not fast; instead is more like an irregular fall-rise succession until stability is reached (Fig. 2) (Oprittov et al. 1991; Vodeneev et al. 2011; Sukhov et al. 2013). The VPs are generated when the plant suffers critical damage, where tissue or structures are severely affected. An open flame exposure is a universal stimulus that will cause this type of signal, even in different plant species (Sukhov et al. 2012; Gallé et al. 2013; Sukhov 2016). In the case of mechanical damage (punction, cutting, flattening), not in all plant species, VPs are registered; for instance, in *Lycopersicon esculentum*, despite wounds, no ES was sensed (Rhodes et al. 1999).

SPs are the type of signal less studied according to the literature. This type of signal is related to APs and VPs because one of these signals is normally on course; for example, during the refractory period, plant's stimulated area, the SPs occurs (Zimmermann et al. 2009). The SPs' difference respect to the other signals is that they are propagated through channels where the others do not, as apoplast (Zimmermann et al. 2009). This type of ES will be generated when plants face stress as insect attack, mechanical damage, light color changes, fire damage and temperature variations (Eschrich et al. 1988; Lautner et al. 2005; Zimmermann et al. 2016; Vuralhan-Eckert et al. 2018).

### 3 Electrical signal influence in plant physiology

Several types of research exhibit the influence of ES in the physiological processes of the plant. The first evidence of this was found in the plant's study with

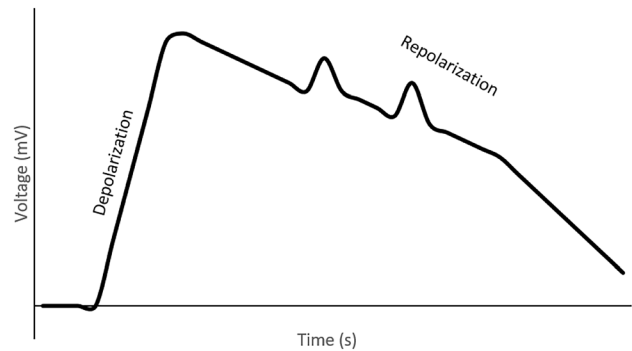


**Fig. 1** Ions flux through the cell membrane during an Action potential and the voltage curve that represents the two phases. **a** The flow of  $\text{Ca}^{2+}$  into the cell membrane inactivates  $\text{H}^+$ -ATPase. **b** The change of potential inactivates  $\text{Ca}^{2+}$  channels and activates  $\text{K}^+$  depending channels. **c** The voltage curve of the APs is a singular and fast spike

evident movement presented in “Carnivorous plants” (*Dionaea*, *Aldrovanda*, and *Drosera*). In these plants, the close of the trap leaves and the subsequent signaling pathways (Jasmonic Acid) related to enzymes synthesis for the prey digestion are activated by APs (Pavlovic et al. 2017; Krausko et al. 2017; Hedrich and Neher 2018). Another plant with evident movement is *Mimosa*, it has the peculiarity that the leaves move to a vertical position, grouping together

when the plant faces mechanical contact. This movement is induced by APs and VP and could have the objective of protecting the leaves from insect attacks, violent wind, or rain (Sibaoka 1991; Fromm and Lautner 2007; Gallé et al. 2015). ES also influence plant respiration. The rate may increase or decrease after the plant faces a stimulus as heating/cooling and salt exposure in *Vicia faba* and APs signals are generated (Filek and Koscielniak 1997). Pruning or the exposure to electrical stimuli has an increasing effect on respiration ratio when VPs signals are generated, as seen in *Conocephalum conicum* (Trebacz et al. 2006). VPs signals induced by burning were related to respiration ratio affection in *Pelargonium zonale*, *Cucurbita* sp. and *Pisum sativum* (Sukhov et al. 2012, 2014a; Sherstneva et al. 2015). The process of photosynthesis is affected by several factors, including ES. A large amount of research shows that the generation of ES can induce a fast photosynthesis inactivation. In *Chara corallina*, APs induced by electrical stimulation inactivates photosynthesis (Bulychev et al. 2004; Krupenina and Bulychev 2007; Krupenina et al. 2008). In *Dionaea muscipula*, the physical stimulation of the mechano-sensitive filaments in the trap leaves generates an APs that causes the trap closure and the inactivation of photosynthesis (Pavlovic et al. 2017). The same effect can be seen with VPs in *Mimosa pudica* after being heated (Lautner et al. 2014), in *Populus* sp., *Pelargonium graveolens*, *Pisum sativum*, and *Zea mays* after being burned (Lautner et al. 2005; Sukhov et al. 2008, 2012; Sukhova et al. 2018; Vuralhan-Eckert et al. 2018). Nevertheless, not always the generation of ES carries an inactivation effect in photosynthesis, in some cases, depending on the type of stimuli that could happen or not. If *Zea mays* and *Populus* sp. are faced with freezing APs will be generated, but the photosynthesis will not be inactivated (Lautner et al. 2005; Fromm et al. 2013). Another physiological aspect where ES has influence is in the pollination of flowers; at the moment that the stigma is stimulated, several signals of APs are generated and propagated through the ovary, preparing it for fertilization in plants of *Hibiscus* sp. and *Incarvillea* sp. (Fromm et al. 1995; Dziubinska 2003). The phytohormones that the plant produces as a response to stress also present relation with the ES. In plants of *Solanum tuberosum* and *Solanum lycopersicum* was found a possible relation between the generation of electrical signals (APs,

**Fig. 2** Voltage curve of a variation potential. Unlike APs, the VPs curve is not a singular and fast spike, the time of depolarization and repolarization is longer, also, several smaller spikes could be seen, depending of stimulus intensity



VPs), due to mechanical wounding, electrical stimulation, and burning, with the production of abscisic acid (ABA) and jasmonic acid (JA) (Peña-Cortés et al. 1995; Herde et al. 1996). In *Pisum sativum* a VPs signal is related to a JA concentration increase after a leaf is burned (Ladeynova et al. 2020). The gene expression can be seen as the most important process provoked by stimuli in the plant, where ES are generated. *Solanum lycopersicum* and *Solanum tuberosum* APs induced by electrical stimulation and VPs induced by fire damage can evoke *pin2* gene expression (Herde et al. 1995, 1996; Stankovic and Davies 1996). In *Solanum tuberosum* the APs generated by heating induced *pin2* gene expression (Fisahn et al. 2004). In *Arabidopsis thaliana*, APs induced by electrical stimulation and VPs induced by wounding stimulated the expression of genes associated with insect defense (Mousavi et al. 2013).

#### 4 Electrical signal analysis and classification due to stress

The ES could be a plant condition indicator; this due to the relation of certain types of ES and specific stress conditions as seen before; derived from this information, other kinds of research arose. As mentioned before, all types of ESs are voltage–time relations; in other words, the description of the behavior of the voltage value through time. This kind of information can be analyzed and classified by applying AI and mathematical algorithms.

Mathematical models have been made to describe the mechanisms that are already studied and to help in the understanding of the complete process of ES occurrence. For APs was made a model that describes the moment of the signal generation based on the

previous physiological process; moreover, it's described using 4 equations, the plasma membrane transporters, tonoplast participation, the active and passive ion transport, the ion passage probability, and evidence of the high importance of the vacuolar area in the signal generation (Novikova et al. 2017). Another mathematical model for APs describes the propagation mechanisms, contributing to theoretical analysis of the intercellular conductivity and H(+)-ATPase relation (Sukhov et al. 2011). For VPs, some mathematical models have also been made. As a first stage a former model simulated the principal characteristics of the signal propagation as ion flux through the plasma membrane, and the possible participation of hydraulic damage-related signals and the influence in the signal features by the damage intensity (Sukhov et al. 2013). Based on the previous model mentioned, the second stage contributes to the possible relation between pH changes and photosynthetic response during VPs propagation (Sherstneva et al. 2016).

Other research works focus on identifying the stress or stimuli that the plant is facing from the signal observed. Usually, AI, statistical information, and other algorithms are used. Some of these works are listed in Table 2, an algorithm (96% accuracy) that detects, describes, and classifies possible APs waveforms, which considers frequency and time domain. It employs nonlinear analysis and statistical information, through AI as Backpropagation Artificial Neural Network (BP-ANN) with an 84.8% of accuracy, Support Vector Machines (SVM) with a 78.2% of accuracy, and Deep learning with 77.4% (Chen et al. in 2016). Signals in Leaves of *Zea mays* plants were measured after periods of water stress; the signal was analyzed employing wavelet transform (WT) and Discrete Fourier Transform (DFT); this work concludes that some parameters related to ES occurrence



**Table 2** Techniques employed for ES identification and classification due to a specific stress or stimuli

Technique	Stress or stimuli associated	Plant species	References
Algorithm and (AI)	Electrical stimulation	<i>Cucumis sativus</i>	Chen et al. in (2016)
Frequency analysis with DFT and WT	Osmotic stress (Drought)	<i>Zea mays</i>	Zhang et al. (2012)
MLA, IA	Low temperature	<i>Glycine max</i>	Pereira et al. (2018)
	Deficient light		
	Osmotic stress		
AI	Salt	<i>Triticum</i> sp.	Qin et al. (2020)
Discriminant analysis and statistical features	Chemical damage (H <sub>2</sub> SO <sub>4</sub> , O <sub>3</sub> , NaCl)	<i>Solanum lycopersicum</i>	Chatterjee et al. (2015)
A decision tree based multi-class classification strategy	Chemical damage (H <sub>2</sub> SO <sub>4</sub> , O <sub>3</sub> , NaCl)	–	Chatterjee et al. (2017)
Binary classifier	Drought	<i>Olea europaea</i> L.	Comparini et al. (2020)

during osmotic stress that can be sensed could be used as a sensor of water demand in plants (Zhang et al. 2012). In other work for the classification of ES according to the type of stress, different techniques of identification as Machine Learning Algorithms (MLA) and Interval Arithmetic (IA) were used, plants of *Glycine max* were exposed to low temperature, deficient light, and osmotic stress, this work concludes that IA is a better technique than MLA for the ES classification in plants (Pereira et al. 2018). A one-dimensional convolutional neural network was used to identify salt stress signals in seedlings of *Triticum* sp. to classify ES related to salt tolerance, achieving a 92.31% accuracy (Qin et al. 2020). In other examples, the discriminant analysis combined with different statistical features was used for ES classification due to stress type; work concludes that diverse statistical features can be used to differentiate the stress or stimuli (Chatterjee et al. 2015). Finally, to identify the Drought stress intensity in *Olea europaea* L., they were exposed to three different irrigation regimes. Later ES was sensed and analyzed by a binary classifier method, achieving a complete plant water condition monitoring (Comparini et al. 2020).

## 5 Application of electricity expecting a response

In the plant physiology area, not only the electricity produced by the own plant is an object of study. Also has been observed the physiological effect of electrical

current or voltage applied to plants. In *Cucumis sativus*, the application of 0.5–3 mA increased ethylene production; at this work the electricity is used as a stress source (Inaba et al. 1991). In *Pisum sativum*, were applied 30–100 mA. Consequently, an increase of phytoalexin (pisatin) was observed; at this work, the electricity is used as an elicitor for plant compounds production (Kaimoyo et al. 2008). In *Amaranthus hypochondriacus*, a current of 500 mA was applied and observed changes in antioxidant enzymatic activities and in the total content of flavonoids (Ozuna et al. 2017). The exposure to low voltage, as 1–6 V, accelerates the growth rate in *Vigna mungo* and has an increasing effect on the fresh weight of roots and young plants of *Solanum tuberosum* (Mizuguchi et al. 1994; Ward 1996). Voltage and current exposure generate ion flux, ion channels activation, and electrical signals propagation through the plant; these could be the most common results of the electricity application, and because of that, the electricity application is a constant technique to generate APs (Black et al. 1971; Fromm and Span- swick 1993; Stankovic and Davies 1996, 1997; Mishra et al. 2001; Dziubińska et al. 2001; Krol et al. 2006; Favre and Agosti 2007; Volkov et al. 2011, 2013, 2019). In the works of Table 3, electricity is used as a source to stress to plants, such as are the cold, fire, mechanical damage, insect attack, and so on. Electricity can be classified as an elicitor (Kaimoyo et al. 2008), a compound that can trigger a defense system in the plant or stimulate metabolism (Alvarado

**Table 3** Application of electricity to plants expecting physiological responses.

Electrical stimulation		Effect in the plant	Plant species	References
Voltage	Low (0.25–2 V)	Trap closure, Induction of electrotonic potentials, Activation of ion channels, Increase in growth rate, Electrical signal propagation	<i>Dionaea muscipula</i> , <i>Aloe vera</i> L., <i>Brassica oleracea</i> L., <i>Lycopersicon esculentum</i> , <i>Arabidopsis thaliana</i> , <i>Mimosa pudica</i> , <i>Vigna mungo</i> , <i>Helianthus annuus</i>	Volkov et al. (2007, 2011, 2013, 2019) Mizuguchi et al. (1994) Dziubińska et al. (2001)
	High (3–18 V)	Initiation of Pin2 mRNA accumulation, increase of abscisic acid, Generation of electrical signals APs generation, Increase weight in fresh sprout and root	<i>Solanum lycopersicum</i> <i>Solanum phureja</i> <i>Salix viminalis</i> L., <i>Solanum tuberosum</i> <i>Dionaea muscipula</i> <i>Arabidopsis thaliana</i>	Herde et al. (1995, 1996) From and Spanswick (1993) Stankovic and Davies (1996, 1997) Ward (1996) Krol et al. (2006) Favre and Agosti (2007)
Current	Low (3 $\mu$ A–300 mA)	Activation of ion channels, Increase of Ethylene production and secondary metabolites, Electrical signal propagation	<i>Solanum lycopersicum</i> <i>Cucumis sativus</i> , <i>Sorghum bicolor</i> , <i>Cicer arietinum</i> , <i>Medicago truncatula</i>	Black et al. (1971) Inaba et al. (1991) Mishra et al. (2001) Kaimoyo et al. (2008)
	High (500–1000 mA)	Increase of phenol content, antioxidant activity, anthocyanins and enzymatic activities	<i>Raphanus sativus</i> <i>Amaranthus hypochondriacus</i>	Dannehl et al. (2009) Ozuna et al. (2017)

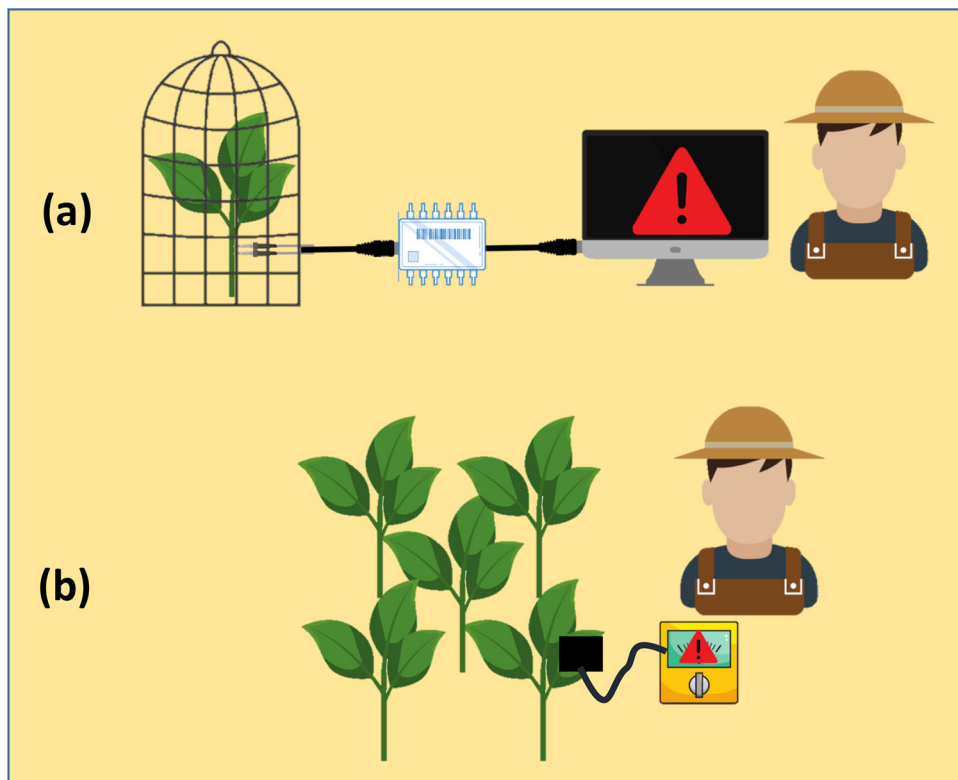
The list is divided by the type of electrical stimuli applied: voltage (classified in low values under 2 V and high values above 3 V) and current (classified in low values under 300 mA and high values above 500 mA). The classification was made according the number of investigations that used similar ranges

et al. 2019). Even the application of electricity has an effect on the plants as compounds synthesis or growing stimuli, none of the researches listed in Table 3 apply an electrical stimulus to plants similar to those electrical signals that occur inside the plants; in other words, there is no assurance that the characteristics of the electricity applied to the plants (Voltage, current) are similar to the voltage or current values, through the time, that the plants generate; generally, these values are chosen arbitrarily and justly accomplishing the condition of non-lethality.

## 6 Perspectives in the electrical signals field

The benefits that the ES study could contribute to crop and plant production are abundant. As seen in this work, the ES can be related to specific stress sources or conditions in the plant; these could be used as diagnostic elements in evaluating plant health. As in any production chain and even more in the food industry, the soon notice of a problem allows a fast answer and a reduction in any threat's negative impact. Nevertheless, the methodologies for the caption of the signals are not exactly practical; the most common technique consists of the insertion of electrodes in the plant (stem or branches); usually, plants are placed under a Faraday cage to avoid





**Fig. 3** **a** The usual methodology for ES capture in plants is a process that requires time to be setting plant by plant. **b** Given the results of recent research, physical properties that can be

measured with hand-meters could be used as indicator of ES presence and relate it to a specific stress, allowing a fast response

electrical interference and are used diverse hardware and software for the signal recording in succession as seen in Fig. 3a (Wildon et al. 1992; Stankovic and Davies 1996; Retivin et al. 1997; Stankovic et al. 1998; Lautner et al. 2005; Krol et al. 2006; Saraiva et al. 2017; Volkov and Shtessel 2017; Simmi et al. 2020; Comparini et al. 2020; Tinturier et al. 2020; Silva et al. 2021). The usual methodology presents the disadvantage of a complex assembly. Once the electrodes are inserted in the plant, a period of time for the signal capture must pass due to the ES generated by the damage done with the electrodes (Volkov and Haack 1995), and the measurement must be done plant by plant. The method seems to be difficult to be applied on field plants; however, some recent research suggests a relation between ES and changes in the reflectance of the leaves. In plants of *Pisum sativum*, VPs induced by burning were related to modifications in the photochemical reflectance (in a range between 400 and 800 nm) due to photosynthetic changes minutes after the stimulus (Sukhov et al.

2019a, b; Sukhova et al 2019, 2020). Reflectance is a physical property of plant leaves related to chlorophyll content affected by water content, nutrients, N content, and diseases (Zebarth et al. 2009; Muñoz-Huerta et al. 2013; Rustioni and Bianchi 2021). Given these relations, many technologies have been developed for a fast in-field chlorophyll lecture and determination of many nutrient contents. For example, in N determination based on leaves' reflectance and transmittance, hand-meters have been used as the SPAD-502 (Gromaz et al. 2017), or GreenSeeker equipment (Friedel et al. 2020). These are small-size devices that place a leaf into a chamber (without removing it from the plant or damaging the leaf). It is exposed to lights of different lengths, and several readings are calculated (Xiong et al. 2015). If ES generated by specific stress is related to specific reflectance values, they could be measured by one of these hand-meters, so the farmer could know at the moment, without the difficulty of electrodes insertion, if there is a problematic situation and have a fast reaction (Fig. 3b).

Another possible benefit of the ES study is related to the fact that the signals in the plants could trigger many defense mechanisms. As seen before in the works listed in Table 3, if electricity is applied to plants, a response will be observed in chemical compounds production, growing ratio increase, and APs generation (Ward 1996; Ozuna et al. 2017; Volkov et al. 2019). Nevertheless, there is no report about a direct triggering effect in defense mechanisms due to electrical stimulation. It must be mentioned that there is no report proving that the values of voltage and current that were applied in the works in Table 3 are similar or related to the ES that the plants generate. The question arises: what would happen if an electrical signal, similar in voltage and current values to the ones that the plant generates under specific stress, is applied to a plant free of that stress? Could an artificial signal, similar to those generated by plants, trigger better those defense mechanisms? And if so, would the plant be prepared to face the specific stress without being exposed to it? Several experiments are required to answer those questions.

## 7 Conclusions

The study of electrical signals could open new techniques and technologies that would bring benefits to agriculture. They help solve several important food production problems: excessive resource expenditure, contamination caused by agrochemicals, quality in crop, and yield. The electrical signals could be used as a problem indicator in plants and could stimulate and obtain desirable agronomical and biotechnological responses from the plants. Nevertheless, several experiments are required to find easier and practical methodologies for ES caption, application, and study, also, nowadays is missing other experiments to evaluate the effect of electrical signals that “mimic” the electrical signals generated inside the plants, on genetic expression, metabolites generation, physiological variables, etc.

## References

- Alvarado AM, Aguirre-Becerra H, Vázquez-Hernández MC, Magaña-Lopez E, Parola-Contreras I, Caicedo-Lopez LH, Contreras-Medina LM, Garcia-Trejo JF, Guevara-Gonzalez RG, Feregrino-Perez AA (2019) Influence of elicitors and eustressors on the production of plant secondary metabolites. Natural bio-active compounds. Springer, Singapore, pp 333–388
- Babikova Z, Johnson D, Bruce T, Pickett J, Gilbert L (2013) How rapid is aphid-induced signal transfer between plants via common mycelial networks? Commun Integr Biol 6(6):e25904. <https://doi.org/10.4161/cib.25904>
- Baldwin IT, Schultz JC (1983) Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. Science 221:277–279
- Black JD, Forsyth FR, Fensom DS, Ross RB (1971) Electrical stimulation and its effects on growth and ion accumulation in tomato plants. Can J Bot 49(10):1809–1815. <https://doi.org/10.1139/b71-255>
- Bowles DJ (1990) Defence-related proteins in higher plants. Annu Rev Biochem 59:873–907
- Bulychev AA, Krupenina NA (2010) Inactivation of plasmalemma conductance in alkaline zones of *Chara corallina* after generation of action potential. Biochem Mosc Suppl Ser A 4:232–239. <https://doi.org/10.1134/S1990747810020169>
- Bulychev AA, Kamzolnikina NA, Luengviriya J, Rubin AB, Müller SC (2004) Effect of a single excitation stimulus on photosynthetic activity and light-dependent pH banding in *Chara* cells. J Membr Biol 202(1):11–19. <https://doi.org/10.1007/s00232-004-0716-5>
- Cerabolini B, Andreis R, Ceriani RM, Pierce S, Raimondi B (2004) Seed germination and conservation of endangered species from the Italian Alps: *Physoplexis comosa* and *Primula glaucescens*. Biol Conserv 117(3):351–356. <https://doi.org/10.1016/j.biocon.2003.12.011>
- Chatterjee SK, Das S, Maharatna K, Masi E, Santopolo L, Mancuso S, Vitaletti A (2015) Exploring strategies for classification of external stimuli using statistical features of the plant electrical response. J R Soc Interface 12(104):20141225–20141225. <https://doi.org/10.1098/rsif.2014.1225>
- Chatterjee SK, Das S, Maharatna K, Masi E, Santopolo L, Colzi I, Mancuso S, Vitaletti A (2017) Comparison of decision tree based classification strategies to detect external chemical stimuli from raw and filtered plant electrical response. Sens Actuators B 249:278–295. <https://doi.org/10.1016/j.snb.2017.04.071>
- Chen Y, Zhao DJ, Wang ZY, Wang ZY, Tang G, Huang L (2016) Plant electrical signal classification based on waveform similarity. Algorithms 9:1–23. <https://doi.org/10.3390/a9040070>
- Chhaya, Yadav B, Jogawat A, Gnanasekaran P, Kumari P, Lakra N, Lal SK, Pawar J, Lal SK, Pawar J, Narayan, OP (2020) An overview of recent advancement in phytohormones-mediated stress management and drought tolerance in crop plants. Plant Gene. <https://doi.org/10.1016/j.plgene.2020.100264>
- Comparini D, Masi E, Pandolfi C, Sabbatini L, Dolfi M, Morosi S, Mancuso S (2020) Stem electrical properties associated with water stress conditions in olive tree. Agric Water Manag 234:106109. <https://doi.org/10.1016/j.agwat.2020.106109>

- Dannehl D, Huyskens-Keil S, Eichholz I, Ulrichs C, Schmidt U (2009) Effects of intermittent-direct-electric-current (IDC) on polyphenols and antioxidant activity in radish (*Raphanus sativus* L.) during growth. *J Appl Bot Food Qual* 83(1):54–59
- Degli Agosti R (2014) Touch-induced action potentials in *Arabidopsis thaliana*. *Arch Sci* 67:125–138. <https://doi.org/10.1093/aob/mcx155>
- Delatorre C, Rodriguez A, Rodriguez L, Majada JP, Ordas RJ, Feito I (2017) Hormonal profiling: development of a simple method to extract and quantify phytohormones in complex matrices by UHPLC–MS/MS. *J Chromatogr B* 1040:239–249
- de Toledo GRA, Parise AG, Simmi FZ et al (2019) Plant electrome: the electrical dimension of plant life. *Theor Exp Plant Physiol* 31:21–46. <https://doi.org/10.1007/s40626-019-00145-x>
- Dziubińska H (2003) Ways of signal transmission and physiological role of electrical potential in plants. *Act Soc Bot Polon* 72:309–318. <https://doi.org/10.5586/asbp.2003.040>
- Dziubińska H, Trębacz K, Zawadzki T (2001) Transmission route for action potentials and variation potentials in *Helianthus annuus* L. *J Plant Physiol* 158(9):1167–1172. [https://doi.org/10.1078/s0176-1617\(04\)70143-1](https://doi.org/10.1078/s0176-1617(04)70143-1)
- Egamberdieva D, Wirth SJ, Alqarawi AA, Abd\_Allah EF, Hashem A (2017) Phytohormones and beneficial microbes: essential components for plants to balance stress and fitness. *Front Microbiol*. <https://doi.org/10.3389/fmicb.2017.02104>
- Eschrich W, Fromm J, Evert RF (1988) Transmission of electric signals in sieve tubes of zucchini plants. *Bot Acta* 101:327–331. <https://doi.org/10.1111/j.1438-808677.1988.tb00052.x>
- Favre P, Agosti RD (2007) Voltage-dependent action potentials in *Arabidopsis thaliana*. *Physiol Plant*. <https://doi.org/10.1111/j.1399-3054.2007.00954.x>
- Felle HH, Zimmermann MR (2007) Systemic signalling in barley through action potentials. *Planta* 226:203–214. <https://doi.org/10.1007/s00425-006-0458-y>
- Filek M, Koscielniak J (1997) The effect of wounding the roots by high temperature on the respiration rate of the shoot and propagation of electric signal in horse bean seedlings (*Vicia faba* L. minor). *Plant Sci* 123:39–46
- Fisahn J, Herde O, Willmitzer L, Peña-Cortés H (2004) Analysis of the transient increase in cytosolic Ca<sup>2+</sup> during the action potential of higher plants with high temporal resolution: requirement of Ca<sup>2+</sup> transients for induction of jasmonic acid biosynthesis and PINII gene expression. *Plant Cell Physiol* 45(4):456–459. <https://doi.org/10.1093/pcp/pch054>
- Friedel M, Hendgen M, Stoll M, Löhnertz O (2020) Performance of reflectance indices and of a handheld device for estimating in-field the nitrogen status of grapevine leaves. *Aust J Grape Wine Res* 26(2):110–120
- Fromm J, Bauer T (1994) Action potentials in maize sieve tubes change phloem translocation. *J Exp Bot* 45:463–469. <https://doi.org/10.1093/jxb/45.4.463>
- Fromm J, Eschrich W (1988a) Transport processes in stimulated and non-stimulated leaves of *Mimosa pudica*. I. The movement of <sup>14</sup>C-labelled photoassimilates. *Trees* 2:7–17
- Fromm J, Eschrich W (1988b) Transport processes in stimulated and non-stimulated leaves of *Mimosa pudica*. II. Energetics and transmission of seismic stimulations. *Trees* 2:18–24
- Fromm J, Eschrich W (1988c) Transport processes in stimulated and non-stimulated leaves of *Mimosa pudica*. III. Displacement of ions during seismonastic leaf movements. *Trees* 2:65–72
- Fromm J, Fei H (1998) Electrical signaling and gas exchange in maize plants of drying soil. *Plant Sci* 132:203–213
- Fromm J, Lautner S (2007) Electrical signals and their physiological significance in plants. *Plant Cell Environ* 30:249–257. <https://doi.org/10.1111/j.1365-3040.2006.01614.x>
- Fromm J, Spanswick R (1993) Characteristics of action potentials in willow (*Salix viminalis* L.). *J Exp Bot* 44(7):1119–1125. <https://doi.org/10.1093/jxb/44.7.1119>
- Fromm J, Hajirezaei M, Wilke I (1995) The biochemical response of electrical signaling in the reproductive system of Hibiscus plants. *Plant Physiol* 109(2):375–384
- Fromm J, Meyer A, Weissenel MH (1997) Growth, membrane potential and endogenous ion currents of willow (*Salix viminalis*) roots are all affected by abscisic acid and spermine. *Physiol Plant* 99:529–537. <https://doi.org/10.1111/j.1399-3054.1997.tb05353.x>
- Fromm J, Hajirezaei MR, Becker VK, Lautner S (2013) Electrical signaling along the phloem and its physiological responses in the maize leaf. *Front Plant Sci* 4:239. <https://doi.org/10.3389/fpls.2013.00239>
- Gallé A, Lautner S, Flexas J, Ribas-Carbo M, Hanson D, Roesgen J, Fromm J (2013) Photosynthetic responses of soybean (*Glycine max* L.) to heat-induced electrical signalling are predominantly governed by modifications of mesophyll conductance for CO<sub>2</sub>. *Plant Cell Environ* 36:542–552. <https://doi.org/10.1111/j.1365-3040.2012.02594.x>
- Gallé A, Lautner S, Flexas J, Fromm J (2015) Environmental stimuli and physiological responses: the current view on electrical signaling. *Environ Exp Bot* 114:15–21. <https://doi.org/10.1016/j.envexpbot.2014.06.013>
- Gilroy S, Białasek M, Suzuki N, Górecka M, Devireddy AR, Karpiński S, Mittler R (2016) ROS, calcium, and electric signals: key mediators of rapid systemic signaling in 1388 plants. *Plant Physiol* 171:1606–1615. <https://doi.org/10.1104/pp.16.00434>
- Gromaz A, Torres JF, San Bautista A, Pascual B, López-Galarza S, Maroto JV (2017) Effect of different levels of nitrogen in nutrient solution and crop system on nitrate accumulation in endive. *J Plant Nutr* 40(14):2045–2053
- Hedden P (2019) A novel gibberellin promotes seedling establishment. *Nat Plants* 5(5):459
- Hedrich R, Neher E (2018) Venus flytrap: how an excitable, carnivorous plant works. *Trends Plant Sci* 23:220–234. <https://doi.org/10.1016/j.tplants.2017.12.004>
- Herde O, Fuss H, Peña-Cortés H, Fisahn J (1995) Proteinase inhibitor II gene expression induced by electrical stimulation and control of photosynthetic activity in tomato plants. *Plant Cell Physiol* 36(4):737–742
- Herde O, Atzorn R, Fisahn J, Wasternack C, Willmitzer L, Peña-Cortés H (1996) Localized wounding by heat initiates the accumulation of proteinase inhibitor II in abscisic acid-

- deficient plants by triggering jasmonic acid biosynthesis. *Plant Physiol* 112(2):853–860
- Hlaváčková V, Krchňák P, Nauš J, Novák O, Špundová M, Strnad M (2006) Electrical and chemical signals involved in short-term systemic photosynthetic responses of tobacco plants to local burning. *Planta* 225(1):235–244. <https://doi.org/10.1007/s00425-006-0325-x>
- Inaba A, Gao JP, Nakamura R (1991) Induction by electric currents of ethylene biosynthesis in cucumber (*Cucumis sativus* L.) fruit. *Plant Physiol* 97(3):1161–1165. <https://doi.org/10.1104/pp.97.3.1161>
- Kaimoyo E, Farag MA, Sumner LW, Wasmann C, Cuello JL, VanEtten H (2008) Sub-lethal levels of electric current elicit the biosynthesis of plant secondary metabolites. *Biotechnol Prog* 24(2):377–384. <https://doi.org/10.1021/bp0703329>
- Katicheva L, Sukhov V, Akinchits E, Vodenev V (2014) Ionic nature of burninduced variation potential in wheat leaves. *Plant Cell Physiol* 55:1511–1519. <https://doi.org/10.1093/pcp/pcu082>
- Katicheva L, Sukhov V, Bushueva, A, Vodenev V (2015) Evaluation of the open time of calcium channels at variation potential generation in wheat leaf cells. *Plant Signal Behav* 10(3):e993231. <https://doi.org/10.4161/15592324.2014.993231>
- Kisnieriene V, Lapeikaite I, Sevriukova O, Ruksenas O (2016) The effects of Ni<sup>2+</sup> on electrical signaling of *Nitellopsis obtusa* cells. *J Plant Res* 129:551–558. <https://doi.org/10.1007/s10265-016-0794-3>
- Kisnieriene V, Lapeikaite I, Pupkis V (2018) Electrical signalling in *Nitellopsis obtusa*: potential biomarkers of biologically active compounds. *Funct Plant Biol* 45:132–142. <https://doi.org/10.1071/FP16339>
- Krausko M, Perutka Z, Sebelá M, Samajová O, Samaj J, Novák O, Pavlovič A (2017) The role of electrical and jasmonate signalling in the recognition of captured prey in the carnivorous sundew plant *Drosera capensis*. *New Phytol* 213:1818–1835. <https://doi.org/10.1111/nph.14352>
- Krol E, Dziubinska H, Stolarz M, Trebacz K (2006) Effects of ion channel inhibitors on cold- and electrically-induced action potentials in *Dionaea muscipula*. *Biol Plant* 50:411–416. <https://doi.org/10.1007/s10535-006-0058-5>
- Krupenina NA, Bulychiev AA (2007) Action potential in a plant cell lowers the light requirement for non-photochemical energy-dependent quenching of chlorophyll fluorescence. *Biochim Biophys Acta* 1767:781–788
- Krupenina NA, Bulychiev AA, Roelfsema MRG, Schreiber U (2008) Action potential in Chara cells intensifies spatial patterns of photosynthetic electron flow and non-photochemical quenching in parallel with inhibition of pH banding. *Photochem Photobiol Sci* 7(6):681–688. <https://doi.org/10.1039/B802243G>
- Ladeynova M, Mudrilov M, Berezina E, Kior D, Grinberg M, Brilkina A, Sukhov V, Vodenev V (2020) Spatial and temporal dynamics of electrical and photosynthetic activity and the content of phytohormones induced by local stimulation of pea plants. *Plants* 9(10):1364
- Lautner S, Grams TEE, Matyssek R, Fromm J (2005) Characteristics of electrical signals in poplar and responses in photosynthesis. *Plant Physiol* 138:2200–2209. <https://doi.org/10.1104/pp.105.064196>
- Lautner S, Stummer M, Matyssek R, Fromm J, Grams TEE (2014) Involvement of respiratory processes in the transient knockout of net CO<sub>2</sub> uptake in *Mimosa pudica* upon heat stimulation. *Plant Cell Environ* 37:254–260. <https://doi.org/10.1111/pce.12150>
- Li T, Wang ZY, Zhao DJ, Huang L, Wang ZY (2016) Development of a portable multi-channel system for plant physiological signal recording. *Inf Process Agric*. <https://doi.org/10.1016/j.inpa.2016.05.001>
- Mishra NS, Mallick B, Sopory SK (2001) Electrical signal from root to shoot in Sorghum bicolor: induction of leaf opening and evidence for fast extracellular propagation. *Plant Sci* 160(2):237–245. [https://doi.org/10.1016/s0168-9452\(00\)00378-2](https://doi.org/10.1016/s0168-9452(00)00378-2)
- Mizuguchi Y, Watanabe Y, Matsuzaki H, Ikezawa Y, Takamura T (1994) Growth acceleration of bean sprouts by the application of electrochemical voltage in a culturing bath. *Denki Kagaku oyobi Kogyo Butsuri Kagaku* 62(11):1083–1085
- Mousavi SA, Chauvin A, Pascaud F, Kellenberger S, Farmer EE (2013) Glutamate receptor-like genes mediate leaf-to-leaf wound signalling. *Nature* 500:422–426. <https://doi.org/10.1038/nature12478>
- Muñoz-Huerta RF, Guevara-Gonzalez RG, Contreras-Medina LM, Torres-Pacheco I, Prado-Olivarez J, Ocampo-Velazquez RV (2013) A review of methods for sensing the nitrogen status in plants: advantages, disadvantages and recent advances. *Sensors* 13(8):10823–10843
- Nadeem SM, Ahmad M, Zahir ZA, Kharal MA (2016) Role of phytohormones in stress tolerance of plants. *Plant Soil Microbes*. [https://doi.org/10.1007/978-3-319-29573-2\\_17](https://doi.org/10.1007/978-3-319-29573-2_17)
- Novikova EM, Vodenev VA, Sukhov VS (2017) Mathematical model of action potential in higher plants with account for the involvement of vacuole in the electrical signal generation. *Biochem (Mosc) Suppl Ser A* 11(2):151–167. <https://doi.org/10.1134/s1990747817010068>
- Oprítov VA, Pyatygin SS, Retivin VG (1991) Bioelectrogenesis in higher plants. Nauka, Moscow, p 1991
- Oprítov VA, Lobov SA, Pyatygin SS, Mysyagin SA (2005) Analysis of possible involvement of local bioelectric responses in chilling perception by higher plants exemplified by *Cucurbita pepo*. *Russ J Plant Physiol* 52:801–808. <https://doi.org/10.1007/s11183-005-0118-2>
- Ozuna C, Cerón-García A, Elena Sosa-Morales M, Salazar JAG, Fabiola León-Galván M, del Rosario Abraham-Juárez M (2017) Electrically induced changes in amaranth seed enzymatic activity and their effect on bioactive compounds content after germination. *J Food Sci Technol* 55(2):648–657. <https://doi.org/10.1007/s13197-017-2974-0>
- Pavlovič A, Jakšová J, Novák O (2017) Triggering a false alarm: wounding mimics prey capture in the carnivorous Venus flytrap (*Dionaea muscipula*). *New Phytol* 216:927–938. <https://doi.org/10.1111/nph.14747>
- Peña-Cortés H, Fisahn J, Willmitzer L (1995) Signals involved in wound-induced proteinase inhibitor II gene expression in tomato and potato plants. *Proc Natl Acad Sci USA* 92(10):4106–4113. <https://doi.org/10.1073/pnas.92.10.4106>
- Pereira D, Papa J, Saraiva G, Souza G (2018) Automatic classification of plant electrophysiological responses to



- environmental stimuli using machine learning and interval arithmetic. *Comput Electron Agric.* <https://doi.org/10.1016/j.compag.2017.12.024>
- Pikulenko MM, Bulychev AA (2005) Light-triggered action potentials and changes in quantum efficiency of photosystem II in *Anthoceros* cells. *Russ J Plant Physiol* 52:584–590. <https://doi.org/10.1007/s11183-005-0087-5>
- Qin XH, Wang ZY, Yao JP, Zhou Q, Zhao PF, Wang ZY, Huang L (2020) Using a one-dimensional convolutional neural network with a conditional generative adversarial network to classify plant electrical signals. *Comput Electron Agric* 174:105464
- Retivin VG, Opritov VA, Fedulina SB (1997) Generation of action potential induces preadaptation of *Cucurbita pepo* L. stem tissues to freezing injury. *Russ J Plant Physiol* 44:432–442
- Rhodes JD, Thain JF, Wildon DC (1999) Evidence for physiologically distinct systemic signalling pathways in the wounded tomato plant. *Ann Bot* 84:109–116. <https://doi.org/10.1006/anbo.1999.0900>
- Rustioni L, Bianchi D (2021) Drought increases chlorophyll content in stems of *Vitis* interspecific hybrids. *Theor Exp Plant Physiol* 33(1):69–78. <https://doi.org/10.1007/s40626-021-00195-0>
- Saraiva GFR, Ferreira AS, Souza GM (2017) Osmotic stress decreases complexity underlying the electrophysiological dynamic in soybean. *Plant Biol* 19(5):702–708
- Sevriukova O, Kanapeckaite A, Lapeikaite I, Kisnieriene V, Ladygiene R, Sakalauskas V (2014) Charophyte electrogenesis as a biomarker for assessing the risk from low-dose ionizing radiation to a single plant cell. *J Environ Radioact* 136:10–15. <https://doi.org/10.1016/j.jenvrad.2014.04.016>
- Shepherd VA, Beilby MJ, Al Khazaaly SA, Shimmen T (2008) Mechanoperception in *Chara* cells: the influence of salinity and calcium on touchactivated receptor potentials, action potentials and ion transport. *Plant Cell Environ* 31:1575–1591. <https://doi.org/10.1111/j.1365-3040.2008.01866.x>
- Sherstneva ON, Vodeneev VA, Katicheva LA, Surova LM, Sukhov VS (2015) Participation of intracellular and extracellular pH changes in photosynthetic response development induced by variation potential in pumpkin seedlings. *Biochemistry (Mosc.)* 80:776–784. <https://doi.org/10.1134/S0006297915060139>
- Sherstneva ON, Vodeneev VA, Surova LM, Novikova EM, Sukhov VS (2016) Application of a mathematical model of variation potential for analysis of its influence on photosynthesis in higher plants. *Biochem (Mosc) Suppl Ser A* 10(4):269–277. <https://doi.org/10.1134/s1990747816030089>
- Sibaoka T (1991) Rapid plant movements triggered by action potentials. *Bot Mag Tokyo* 104:73–95. <https://doi.org/10.1007/BF02493405>
- Silva FB, da Conceição Oliveira Macedo F, Capelin D et al (2021) Multivariate characterization of spontaneously generated electrical signals evoked by electrical stimulation in abscisic acid mutant tomato plants. *Theor Exp Plant Physiol* 33:15–28. <https://doi.org/10.1007/s40626-020-00191-w>
- Simmi FZ, Dallagnol LJ, Ferreira AS, Pereira DR, Souza GM (2020) Electrome alterations in a plant-pathogen system: toward early diagnosis. *Bioelectrochemistry* 133:107493
- Simura J, Antoniadi I, Siroká J, Tarkowská D, Strnad M, Ljung K, Novak O (2018) Plant hormonomics: multiple phytohormone profiling by targeted metabolomics. *Plant Physiol* 177:476–489
- Stahlberg R, Cleland RE, van Volkenburgh E (2006) Slow wave potentials—a propagating electrical signal unique to higher plants. In: Baluska F, Mancuso S, Volkmann D (eds) *Communication in plants. Neuronal aspects of plant life*. Springer-Verlag, Berlin, pp 291–308
- Stankovic B, Davies E (1996) Both action potentials and variation potentials induce proteinase inhibitor gene expression in tomato. *FEBS Lett* 390(3):275–279. [https://doi.org/10.1016/0014-5793\(96\)00672-2](https://doi.org/10.1016/0014-5793(96)00672-2)
- Stanković B, Davies E (1997) Intercellular communication in plants: electrical stimulation of proteinase inhibitor gene expression in tomato. *Planta* 202(4):402–406
- Stankovic B, Witters DL, Zawadzki T, Davies E (1998) Action potentials and variation potentials in sunflower: an analysis of their relationships and distinguishing characteristics. *Physiol Plant* 103(1):51–58. <https://doi.org/10.1034/j.1399-3054.1998.1030107.x>
- Sukhov V (2016) Electrical signals as mechanism of photosynthesis regulation in plants. *Photosynth Res* 130:373–387. <https://doi.org/10.1007/s11120-016-0270-x>
- Sukhov VS, Pyatygin SS, Opritov VA, Krauz VO (2008) Influence of propagating electrical signals on delayed luminescence in pelargonium leaves: experimental analysis. *Biophysics* 53:226–228. <https://doi.org/10.1134/S0006350908030081>
- Sukhov V, Nerush V, Orlova L, Vodeneev V (2011) Simulation of action potential propagation in plants. *J Theor Biol* 291:47–55. <https://doi.org/10.1016/j.jtbi.2011.09.019>
- Sukhov V, Orlova L, Mysyagin S, Sinitsina J, Vodeneev V (2012) Analysis of the photosynthetic response induced by variation potential in geranium. *Planta* 235:703–712. <https://doi.org/10.1007/s00425-011-1529-2>
- Sukhov V, Akinchits E, Katicheva L, Vodeneev V (2013) Simulation of variation potential in higher plant cells. *J Membr Biol* 246:287–296. <https://doi.org/10.1007/s00232-013-9529-8>
- Sukhov V, Sherstneva O, Surova L, Katicheva L, Vodeneev V (2014a) Proton cellular influx as a probable mechanism of variation potential influence on photosynthesis in pea. *Plant Cell Environ* 37:2532–2541. <https://doi.org/10.1111/pce.12321>
- Sukhov V, Surova L, Sherstneva O, Vodeneev V (2014b) Influence of variation potential on resistance of the photosynthetic machinery to heating in pea. *Physiol Plant* 152:773–783. <https://doi.org/10.1111/ppl.12208>
- Sukhov VS, Gromova EN, Sukhova EM, Surova LM, Nerush VN, Vodeneev VA (2019a) Analysis of correlations between the indexes of light-dependent reactions of photosynthesis and the photochemical reflectance index (PRI) in pea leaves under short-term illumination. *Biochem (Mosc) Suppl Ser A* 13(1):67–77
- Sukhov V, Sukhova E, Gromova E, Surova L, Nerush V, Vodeneev V (2019b) The electrical signal-induced systemic photosynthetic response is accompanied by changes in the photochemical reflectance index in pea. *Funct Plant Biol* 46(4):328–338

- Sukhov V, Sukhova E, Vodeneev V (2019c) Long-distance electrical signals as a link between the local action of stressors and the systemic physiological responses in higher plants. *Prog Biophys Mol Biol* 146:63–84
- Sukhova E, Akinchits E, Sukhov V (2017) Mathematical models of electrical activity in plants. *J Membr Biol* 250:407–423. <https://doi.org/10.1007/s00232-017-9969-7>
- Sukhova E, Mudrilov M, Vodeneev V, Sukhov V (2018) Influence of the variation potential on photosynthetic flows of light energy and electrons in pea. *Photosynth Res* 136(2):215–228. <https://doi.org/10.1007/s11120-017-0460-1>
- Sukhova E, Yudina L, Akinchits E, Vodeneev V, Sukhov V (2019) Influence of electrical signals on pea leaf reflectance in the 400–800-nm range. *Plant Signal Behav* 14(7):1610301
- Sukhova E, Yudina L, Gromova E, Nerush V, Vodeneev V, Sukhov V (2020) Burning-induced electrical signals influence broadband reflectance indices and water index in pea leaves. *Plant Signal Behav* 15(4):1737786
- Szechynska-Hebda M, Lewandowska M, Karpiński S (2017) Electrical signaling, photosynthesis and systemic acquired acclimation. *Front Physiol* 8:684. <https://doi.org/10.3389/fphys.2017.00684>
- Tinturier E, Leblanc-Fournier N, Badel E, Julien JL (2020) Stem bending generates electrical response in poplar. *bioRxiv*
- Trebacz K, Sievers A (1998) Action potentials evoked by light in traps of *Dionaea muscipula* Ellis. *Plant Cell Physiol* 39:369–372. <https://doi.org/10.1093/oxfordjournals.pcp.a029379>
- Trebacz K, Dziubinska H, Krol E (2006) Electrical signals in long-distance communication in plants. *Commun Plants* 277–290. <https://doi.org/10.4161/15592324.2014.993231>
- Vodeneev VA, Opritov VA, Pyatygin SS (2006) Reversible changes of extracellular pH during action potential generation in a higher plant *Cucurbita pepo*. *Russ J Plant Physiol* 53:481–487. <https://doi.org/10.1134/S102144370604008X>
- Vodeneev VA, Akinchits EK, Orlova LA, Sukhov VS (2011) The role of  $\text{Ca}^{2+}$ ,  $\text{H}^+$ , and  $\text{Cl}^-$  ions in generation of variation potential in pumpkin plants. *Russ J Plant Physiol* 58:974–981. <https://doi.org/10.1134/S1021443711050256>
- Vodeneev V, Orlova A, Morozova E, Orlova L, Akinchits E, Orlova O, Sukhov V (2012) The mechanism of propagation of variation potentials in wheat leaves. *J Plant Physiol* 169:949–954. <https://doi.org/10.1016/j.jplph.2012.02.013>
- Vodeneev V, Akinchits E, Sukhov V (2015) Variation potential in higher plants: mechanisms of generation and propagation. *Plant Signal Behav* 10(9):e1057365. <https://doi.org/10.1080/15592324.2015.1057365>
- Volkov AG, Haack RA (1995) Insect-induced bioelectrochemical signals in potato plants. *Bioelectrochem Bioenerg* 37:55–60
- Volkov AG, Shtessel Y (2017) Electrotonic signal transduction between *Aloe vera* plants using underground pathways in soil: experimental and analytical study. *AIMS Biophys* 4:576–595. <https://doi.org/10.3934/biophy.2017.4.576>
- Volkov AG, Adesina T, Markin VS, Jovanov E (2007) Kinetics and mechanism of *Dionaea muscipula* trap closing. *Plant Physiol* 146(2):694–702. <https://doi.org/10.1104/pp.107.108241>
- Volkov AG, Foster JC, Jovanov E, Markin VS (2011) Anisotropy and nonlinear properties of electrochemical circuits in leaves of *Aloe vera* L. *Bioelectrochemistry* 81(1):4–9. <https://doi.org/10.1016/j.bioelechem.2010.11.001>
- Volkov AG, O'Neal L, Volkova-Gugeshashvili MI, Markin VS (2013) Electrostimulation of *Aloe vera* L., *Mimosa pudica* L. and *Arabidopsis thaliana*: propagation and collision of electrotonic potentials. *J Electrochem Soc* 160(7):G3102–G3111. <https://doi.org/10.1149/2.018307jes>
- Volkov AG, Toole S, WaMaina M (2019) Electrical signal transmission in the plant-wide web. *Bioelectrochemistry* 129:70–78
- Vuralhan-Eckert J, Lautner S, Fromm J (2018) Effect of simultaneously induced environmental stimuli on electrical signalling and gas exchange in maize plants. *J Plant Physiol* 223:32–36. <https://doi.org/10.1016/j.jplph.2018.02.003>
- Wang Q, Cai W-J, Yu L, Ding J, Feng Y-Q (2017) Comprehensive profiling of phytohormones in honey by sequential liquid-liquid extraction coupled with liquid chromatography-mass spectrometry. *J Agric Food Chem* 65:575–585
- Ward RG (1996) The influence of electric currents on the growth of tomato plants. *Acta Physiol Plant* 2(18):121–127
- Wildon DC, Thain JF, Minchin PEH, Gubb IR, Reilly AJ, Skipper YD, Doherty HM, O'donnell PJ, Bowles DJ (1992) Electrical signalling and systemic proteinase inhibitor induction in the wounded plant. *Nature* 360(6399):62–65. <https://doi.org/10.1038/360062a0>
- Williams SE, Pickard BG (1972) Properties of action potentials in *Drosera* tentacles. *Planta* 103:193–221
- Williams SE, Pickard BG (1972) Receptor potentials and action potentials in *Drosera* tentacles. *Planta* 103:222–240
- Xiong D, Chen J, Yu T, Gao W, Ling X, Li Y, Peng S, Huang J (2015) SPAD-based leaf nitrogen estimation is impacted by environmental factors and crop leaf characteristics. *Sci Rep* 5(1):1–12
- Zebarth BJ, Drury CF, Tremblay N, Cambouris AN (2009) Opportunities for improved fertilizer nitrogen management in production of arable crops in eastern Canada: a review. *Can J Soil Sci* 89(2):113–132
- Zhang X, Yu N, Xi G, Meng X (2012) Changes in the power spectrum of electrical signals in maize leaf induced by osmotic stress. *Chin Sci Bull* 57(4):413–420. <https://doi.org/10.1007/s11434-011-4820-5>
- Zhao DJ, Chen Y, Wang ZY, Xue L, Mao TL, Liu YM, Wang ZY, Huang L (2015) High-resolution non-contact measurement of the electrical activity of plants in situ using optical recording. *Sci Rep* 5:13425. <https://doi.org/10.1038/srep13425>
- Zimmermann MR, Felle HH (2009) Dissection of heatinduced systemic signals: superiority of ion fluxes to voltage changes in substomatal cavities. *Planta* 229:539–547. <https://doi.org/10.1007/s00425-008-0850-x>
- Zimmermann MR, Maischak H, Mithofer A, Boland W, Felle HH (2009) System  $\epsilon$  potentials, a novel electrical long-distance apoplastic signal in plants, induced by wounding. *Plant Physiol* 149:1593–1600. <https://doi.org/10.1104/pp.108.133884>



Zimmermann MR, Mithofer A, Will T, Felle HH, Furch AC (2016) Herbivore-triggered electrophysiological reactions: candidates for systemic signals in higher plants and the challenge of their identification. *Plant Physiol* 170:2407–2419. <https://doi.org/10.1104/pp.15.01736>

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