Review Paper:

Electrical signaling in plants: Without neurons, a way to regulate and organize

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Abstract

Electrical signaling in plants attracts the attention of both biologists and electrical engineers because of its fast transmission over long distances in plants. Electrical signaling can be intracellular or intercellular. Evidence suggests that such signaling mechanisms can facilitate vital activities in plants such as respiration, photosynthesis, movements as well as water uptake. Electrical signaling operates during stress responses. A local electrical potential is generated during stress responses.

However, the action potential is able to transmit long distances and its role has been experimented in biologically closed circuits of Venus flytrap. Action potential involves influx and efflux of ions. Slow-wave potential occurs during changes in turgor pressure. Conducting tissues such as xylem and phloem also possess appreciable electrical resistance and conductance properties. Xylem is a dead tissue. However, it is able to conduct electrical impulses. In this way, xylem offers unique opportunity for engineers to unravel the mechanisms of electrical signaling in plants. Such research may also resolve multiple issues related to the fact of how plants conduct signals without neurons. Studies on natural sensors and transducers present in different parts of the plants can inspire novel upcoming bio-inspired engineering designs.

Keywords: Action Potential, Electrical signaling, Environmental stress, Plant cells, Xylem.

Introduction

The plant kingdom is unique in multiple aspects which provides a challenging task for engineers and biologists to understand. Plants do not have an immune system but they can survive an infection. Plants do not have pumping systems but they can efficiently transport water several meters above. One of the similar challenging tasks is to unravel the mechanism – How plants communicate within their system? They do not have a nervous system, yet they effectively communicate. Many researchers were drawn to this phenomenon as early as J.C. Bose[2]. His pioneer experiments proposed the idea that plants can communicate, exhibit a nervous system like activity and they are intelligent.

Currently, we know that communication occurs in the form of small electric currents and plants can conduct these currents across long distances. Electrical excitability and associated signaling have emerged as one of the promising areas of transdisciplinary research.

Initially, the electrical signaling has been associated with rapid and visually striking movements, but later the existence has been logically explained in other plants as well[5]. The current review evaluates the latest knowledge associated with electrical signaling in plants.

Electrical signal types in plants

Higher plants effectively utilize electric voltage potential to achieve various tasks such as fast nastic motion, opening and closing of stomata, root behaviour, leaf movements and stress responses (Table 1). Electrical signals have also been correlated with physiological functions[8].

Based on the electric signal generation and its transmittance, it is possible to classify the electrical potential generated in plants into (i) Local electrical potential (ii) Action potential (iii) Variation potential and (iv) System potential.[34,36]

Local electrical potential: The local electrical potential is a sub-threshold potential[34]. This is induced in response to environmental stress[33]. This type of electrical potential is site-specific and is not transmitted across long distances[16]. Such local electric signals are stress induced bioelectrical signals that propagate as a chemical wave[13]. The electric potential has been correlated with physiological mechanisms[9,26]. Local electrode potential is also designated as a wound induced potential, as it is generated in the case of a mechanical injury. This potential is originated and dissipated at the site of stimulation and does not travel long distances[18].

Action potential: The action potential can travel long distances within the plant and is responsible for regulating active movements[11]. Plants possess several touch specific movements and its mechanism involves action potential[21]. Touch specific movements require some minimum intensity of the mechanical stimuli.

Similarly, action potential also requires some minimum amount of triggering force and hence follow all or no law[34]. Transmission of action potential has been coupled with calcium influx into the cytoplasm and efflux of potassium and chloride[5].

Table 1
Few examples of plant responses that are regulated through electrical signalling

Plant processes	Nature of Electrical signaling
Touch specific movements	Action potential and long-distance transmission, associated ion movements[4,21]
Water stress	Electrokinetic effects Xylem electrical impulses[10,12]
Leaf movements	Phloem conducting channels Biologically closed circuits[19,30]
Mechanical injuries - wound	hydraulic and chemical impulses, ion impulses[24,27]

The Venus fly trap circuit is an example of a biologically closed electric circuit which involves the transmission of electric potential. The triggering hairs contain mechanical sensors. Receptor potentials produced on touching these sensors by insects generate electrical potential which serves as action potential[1]. These traps also exhibit the property of electrical memory[30]. An important finding is that when inhibitors of aquaporins, the water-conducting protein channels and voltage-gated channels are used, the action of trap is hindered[29,31]. Research also confirmed the existence of a network that conducts the action potential. It occurs through the plasma membrane and plasmodesmata of the phloem tissue. These networks act as an effective way for long-distance communications and can be termed as nerve-like cellular equipment[28].

The action potential mediated movements are also confirmed in other plants such as *Aldrovanda vesiculosa* and *Drosera*. A cell to cell transfer mechanism of electrotonie has been put forward and investigated[20]. The electrical potential exist for less than a second[6]. This has been utilized by plants to regulate and fine-tune mechanical properties[35].

Water stress and associated electrical impulses: Electrical impulses have been recognized as a physiological parameter in accessing the water stress in plants[3]. Analysis of the electric potential in *Populus nigra* indicated that electrokinetic effects can be correlated with the movement of sap[10]. An experimental investigation has been carried out by an electrode array with electrodes in the trunk as well as in roots along with measurements regarding sap flow confirming the electrokinetic effects. The electrokinetic effect has been linked to the sap flow. The study also revealed that spatio-temporal features of the electric potential may be due to the mechanism that permits diffusion of charge carriers across the xylem vessels[10]. The xylem vessels may have a higher possibility of electrically active units[10].

Long term analysis of the electric potential on xylem vessels indicated that xylem electrical potential is dependent on the water flow rhythms[12]. It has been measured at a range between 50 mV to 200 mV in the xylem vessels of potted *Ficus bennjamia* tree[14]. They also found that there exists no correlation of this voltage with water flow as well as soil ion concentration. These facts lead to the hypothesis that the xylem electrical potential occurs as a result of homeostatic features of the plant[14]. An oscillatory behaviour of electric potential was found in roots. The oscillatory behaviour has been correlated to the electrical resistance existing at the xylem and parenchyma interface of root tissues[25].

Electric potential and leaf movements: A wide spectrum of scientists has been attracted in unravelling the mechanism of touch-me-not *Mimosa pudica* plant. The researches conducted in this regard in non-stimulated, stimulated and relaxed pulvini of mature *Mimosa pudica* confirmed sieve tube, a phloem element that serves as a conducting channel for electric potential. A charged 100 µF capacitor method was developed to evaluate the electrical impulses generated in *Mimosa pudica*[32]. The touch causes the generation of an action potential which is transmitted upto the small pulvinus located below each leaflet[19]. Hence it is a biologically closed circuit[32].

Variation potential in plants: Similar to the action potential, slow-wave potentials (or variation potential) are transmitted across the entire plant[22,23] and hence are long-distance transmitting potentials. Slow-wave potential occurs as a change in turgor pressure. The spreading occurs as membrane potential[22]. In plants, variation potential occurs as a result of damage such as crushing or heating. This damage causes a transient depolarization which arises as a result of the combined activity of hydraulic and chemical impulses[27]. An interesting study involving mathematical modeling and simulation of variation potential in plants provides evidential support towards the diffusion of wound substances along with ion influxes involving calcium ions[24].

System potential: *Vicia faba* and *Horderum vulgare* provided a novel mechanism of long-distance electrical signaling mechanism known as system potential. It is conducted through apoplast and occurs as a result of mechanical injury such as wounding[36]. Some reports confirmed the transmission of signals through conducting tissues such as xylem and phloem[4,17].

Associated mechanisms

The mechano-stimulated electrical signal has been found to be regulating hormonal responses in plants. A rapid change in the electrical field across membrane has been coupled to chemical signaling such as jasmonate or ethylene[7]. This study also confirms the possible interaction between conducting tissues such as xylem and phloem as electro-osmotic coupling. In a study involving wounded cells, it has been confirmed that there occurs a depolarization of membrane which is coupled with calcium ion fluxes. This study revealed a two cell types (sieve tubes and xylem cells) mediated method of electric signaling[15]. Influx and efflux of ions have been found to be associated with electrical signaling[4]. As a result of the fluid flow, buckling, swelling or cavitation of plant parts occur resulting in the mechanical action[11].

Future trends

Plants stand distinct from animals in two aspects: (i) Plants do not have a specialized defence system unlike animals. (ii) Plants do not have conducting-channels like neurons, yet they effectively communicate, control and organize. Engineers understand that unravelling the logical mechanisms of communication within plants is significant towards further product development. A part of these mechanisms involves electrical impulses.

Future trends regarding the research in natural electric potential differences in plants can have dual impacts: (i) Understanding the mechanisms of electrical conductivity, resistance and electro-chemical-mechanical machines of plants and (ii) Bioinspired devices based on the logical design of electricity generation and its effective use by the plants.

Conclusion

Similar to animals, plants also depend on electrical signals for transmission and communication within the organism. However, plants do not have a nervous system, but possess nerve like activities. The electrical signal origin has been correlated to membrane potential. The electrophysiology of plants has provided a unique opportunity for further research. The existence of sensors and conducting channels in plants may provide opportunities for translational bioinspirated designs. Hence the cognitive behaviour of plants needs to be evaluvated further.

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