ISSN 0006-3509, Biophysics, 2016, Vol. 61, No. 3, pp. 505–512. © Pleiades Publishing, Inc., 2016.
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COMPLEX SYSTEMS BIOPHYSICS

Electrical Signals in Higher Plants: Mechanisms of Generation and Propagation

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Received November 11, 2015

Abstract—Local stimulation induces generation and propagation of electric signals in higher plants. Noninvasive stimulus induces an action potential and damaging influences lead to the variation potential. The mechanism of the generation of an action potential is rather complex in nature and is associated with both activation of ion channels (Ca^{2+}, Cl^-, and K^+) and transient change in the activity of the plasma membrane H^+-ATPase. Generation of the variation potential, the duration of which is considerably longer than that of the action potential, is based on transient inactivation of the electrogenic pump; however, passive ion fluxes also contribute to such process, which causes qualitative similarity of the mechanisms of action potential and variation potential generation. Propagation of electrical signals mainly occurs in conducting bundles; thus, transfer of an action potential is associated with vascular parenchyma and sieve elements, while the variation potential is connected to the xylem vessels. The mechanism of the distribution the action potential is similar to nerve impulse transmission, while generation of the variation potential is induced by transfer of a chemical substance, whose propagation is accelerated by a hydraulic wave.

Keywords: action potential, generation, higher plants, propagation, variation potential

DOI: 10.1134/S0006350916030209

INTRODUCTION

The first records of the ability of higher plants to generate electric signals appeared in the late 19th century in the works of the English researcher Burdon–Sanderson, which were performed on the Venus flytrap [1]. The onset of regular investigations of excitability in higher plants is associated with the name Bose. He was the first to experimentally substantiate the possibility of the occurrence and propagation of action potentials (APs) in *Mimosa* conducting tissues [2]. It has been thought for many years that electric pulses that respond to outer stimuli occur only in plants that possess rapid locomotor functions but that other ("ordinary") plants are devoid of this ability. In the 1960's, the action potential was not only discovered in ordinary plants but its propagation was also found to be capable of inducing changes in functional activity [3].

As well, in the early 20th century, a different, slowly spreading, electric reaction of plants was reported. This is caused by leaf squashing, cutting, or scorching [1, 4]. Later, an electric response to scorching was studied in *Mimosa* [1]. In 1935, the term variation potential (VP) was introduced for such slowly spreading electric reactions to damaging factors. A detailed history of investigations of electric signals (ES) in plants has been presented in the works [1, 4, 6].

In recent years, another electric signal type, which is referred to as the systemic potential, was reported [7]. Its main peculiarity is the direction to hyperpolarization, unlike both AP and VP. However, little is known of this type of electric signal.

Contemporary electrophysiology of plants focuses on functional effects induced by electric signals [6, 8–13]. In particular, the characters of diverse responses, mechanisms of conversion of electric signal to functional responses, informative roles and other properties of electric signals are being intensively explored. In this field, the mechanisms of generation and propagation of electric signals are thought to be more or less clear. However, some recent results do not completely conform to the established mechanisms of these phenomena, which requires critical revision of the modern concepts.

GENERAL DATA

An action potential occurs under the influence of stimuli of moderate intensity including mechanical stress, electrical stimulation, gradual or sharp cooling, changes in illumination, etc. [4, 8, 14, 15]. An AP in

Abbreviations: AP, action potential; ES, electric signals; VP, variation potential.

higher plants is known to obey all of the principal lows of excitation, viz., all-or-none occurrence after the achievement of an excitation threshold, the existence of an absolute and a relative refractory period, accommodation phenomenon, etc. [4, 15].

As opposed to an action potential, a variation potential occurs, as a rule, upon scorching with an open flame, contacts with hot objects, and upon gross wounding, such as incision, squashing, and puncture [1, 4, 16]. The variation potential has a long-term uncontrolled phase of depolarization and, especially, repolarization, which gave rise to the term slow wave. The rate of variation potential propagation is usually slower than that of the action potential and may depend on ambient conditions. As well, the variation potential, unlike the action potential, depends on the intensity of an external stimulus: the higher the intensity is the greater the VP amplitude is [4, 16, 17]. Therefore, the properties of APs and VPs significantly differ from each other. This supposes significant differences in the mechanisms of both the generation and propagation of the two signal types.

GENERATION MECHANISM

Action potential generation in excitable cells of either animals or plants is associated with the dramatic (liminal) changes in cell membrane permeability for particular ions. Here, while ion mechanism of AP would be considered as sodium-potassium in animals, it is chloride-potassium in plants [4]. The knowledge of the ion mechanism of AP generation in higher plants rests on the results obtained on giant cells of Characean algae. Due to the large sizes of their cells, these algae are used as model objects, as is the squid giant axon in animal electrophysiology; thus the excitation process is rather well studied in these algae.

Studies on Characean algae have shown that during an impulse, the onset of depolarization occurs via Ca^{2+} influx into the cell, which, in turn, activates chloride channels. The subsequent development of the depolarization phase occurs through an efflux of Cl^- ions, whose electrochemical potential is outward. The repolarization phase of AP is formed by the efflux of K^+ ions that originate from activation of potential-dependent potassium channels [18–21].

The small sizes of excitable cells, the complex structure of the conducting tissue, and plasmadesmal intercellular coupling explain the fact that the nature of an ion current upon excitation is not determined by the conventional method of voltage fixation. To unravel the mechanism of AP generation in higher plants, a set of methods has been used that includes the analysis of electrochemical potential gradients of ions [22], the detection of concentration shifts upon excitation [23–26], as well as inhibitor-based analysis with selective blockers of anion [23, 27, 28], potassium [23, 29], and calcium [24, 30–32] channels. The results of the analyses indicate that in higher plant cells the formation of an AP depolarization phase involves a Ca^{2+} influx and $C1^-$ efflux (ingoing current), whereas the repolarization phase involves K^+ efflux (outgoing current). Hence, the APs are fundamentally similar in higher plants and Characean algae.

However, there are some arguments in favor of another mechanism of AP generation that is associated with reversible inactivation of the H^+-ATPase of plasma membrane [33–35]. In this regard, it has been found that calcium ions inhibit the activity of this enzyme; a certain level of the activity is required to form an action potential [4, 34, 36], AP generation is accompanied by changes in intracellular pH [26, 34], the repolarization phase contains a component related to changes of H^+-ATPase activity [33], etc. Based on these data [34, 37], we offer an extended scheme of AP generation (Fig. 1b). Depolarization down to the excitation threshold level activates potential-dependent Ca^{2+} channels. Calcium, when entering cells, activates Ca^{2+}-dependent (potential-controlled) chloride channels and suppresses H^+-ATPase. The chloride efflux and suppression of H^+-ATPase forms a depolarization phase to the peak level of the AP. The potassium flux, which, presumably starts as early as pulse depolarization, initiates the first step of the repolarization phase to the level of the potassium-equilibrium potential. The H^+-ATPase is then activated, apparently, because of calcium ion removal from the cytoplasm and the rise in potassium concentration in near-membrane space outside the cell. The activated H^+-pump forms the second phase of repolarization, terminating the generation of action potential. This scheme of AP generation was taken as a basis of a mathematical model of the AP [37]. The model showed good compliance with the experimental results and, therefore, supported the hypothesis of H^+-ATPase participation in the development of an action potential.

It should be mentioned here that the H^+-ATPase inactivation does not seem to strongly contribute to the development of the action potential since elimination of this mechanism by means of inhibition of enzyme regulation by calcium ions reduces the action potential amplitude by as little as 10% but such treatment does not absolutely change the extracellular pH [34].

In contrast to the AP, the variation potential is believed to be associated with a transitional change in the activity of electrogenic pump, namely, H^+-ATPase of plasma membrane [7, 17, 38]. This concept follows from (1) data that support the involvement of the H^+-pump in the VP generation [4, 7, 39–44] and (2) data that do not support the contribution of passive ion flows due to activation of ion channels [40, 42, 43, 45]. The first group of facts considers experiments in which substances that modulate H^+-ATPase activity were used [40, 41], the pH of the medium was varied, and

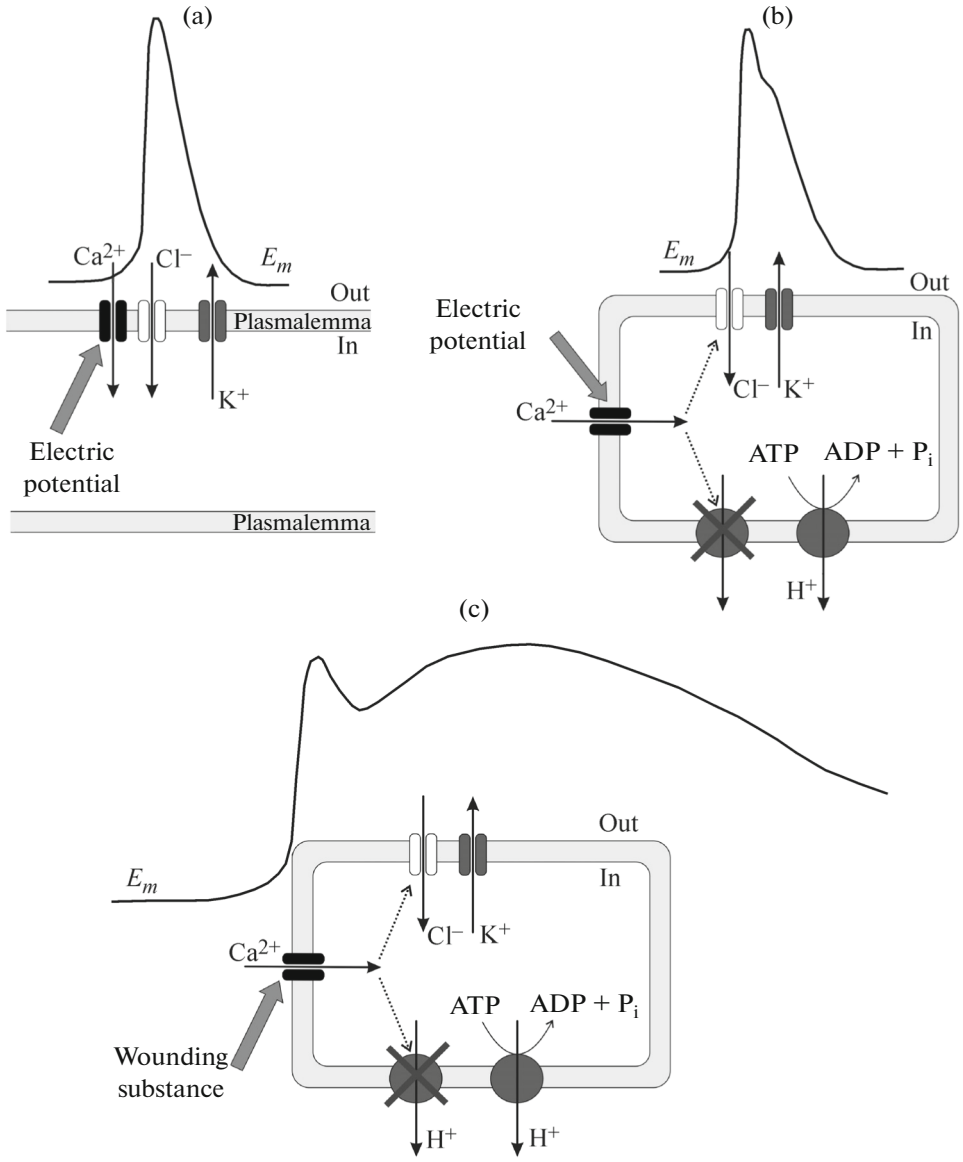

Fig. 1. Schemes of the generation processes of the action potential and variation potential (based on [4, 34, 46]): (a), an action potential in Characean algae; (b), an action potential in higher plants; (c), variation potential.

the proton permeability was increased via protonophores [40, 41]. Suppression of H^+-ATPase and an increase in proton permeability bring about a substantial reduction of the variation potential amplitude down to its abolishment. Recording of the pH time-course inside and outside of cells by potentiometry or pH-sensitive fluorescent probes [7, 44, 45, 47, 48] indicates that transient acidification of the cytoplasm and alkalinization of the apoplast occur during VP generation.

As a separate block, the data may be considered in which the contribution of H^+-ATPase to the VP generation is substantiated by the evidence that does not support the involvement of passive ion flows. In particular, some works [40, 45] showed that VP generation was not accompanied by changes in the input resistance of the plasmalemma and its permeability for K^+, Na^+, Ca^{2+}, and Cl^-. These results support the idea of H^+-ATPase inactivation as a major mechanism of depolarization during the VP, and its reactivation as a major mechanism of repolarization [17, 40, 41, 43, 45].

All the same, a large body of experimental evidence that has accumulated indicates the contribution of passive ion flows to VP generation. The necessity of Ca^{2+} influx for the development of the reaction has been clearly shown because a blockade of calcium channels and Ca^{2+} removal from the intracellular medium considerably suppress (up to the abolish-

ment) the amplitude of the variation potential [40, 43, 44, 46, 49, 50]. Blocking anion channels strongly diminishes the amplitude and the speed of development of depolarization for the VP [40, 43, 44, 46, 49, 50] and VP generation is accompanied by a rapid transient increase in the Cl^- concentration in the intracellular medium [44, 50]. The blockade of potassium channels confirms the contribution of K^+ efflux to the development of the repolarization phase [46]. Another fact should also argues in favor of ion-channel activation, viz., the decrease in plasmalemma resistance that is recorded during the variation potential in wheat seedlings [46].

The sum of the experimental evidence indicates that both transitory changes in H^+-ATPase activity and the activation of ion channels together with the formation of passive fluxes of ions Ca^{2+}, Cl^-, and K^+ are involved in VP generation (Fig. 1c). Therefore, the mechanism of the VP is similar to that of the AP in higher plant cells. If so, the question arises of the origin of the differences in the parameters of the two potential types. It may be assumed that the main difference lies in the reaction initiation. In both types of potential, this stage occurs via calcium ion efflux from the intracellular medium. Here, AP generation is related to the activation of potential-dependent calcium channels [26, 52] while VP generation seems to involve activation of ligand-controlled ion channels [49]. This leads to different timecourses of the calcium cellular contents, which, in turn, creates differences in the dynamics of the activities of anion channels and H^+-ATPase since the transporters of both types are under the control of Ca^{2+}. In fact, the first experimental evidence has been obtained of long-term (tens of seconds) activation of calcium channels during the VP [53]. It should be noted that the proposed scheme of plant cell ion transport, which was used to describe the action potential [37], describes the variation potential as well after the inclusion of an additional element, viz., ligand-controlled calcium channels [49].

THE PROPAGATION MECHANISM

When an action potential spreads over a plant, its amplitude does not dampen; the speed of the spreading remains constant (from several mm/s to several cm/s depending on particular plant species) and fits the cable equation well [4]. This means that AP propagation is an active process in higher plants and its mechanism is generally similar to that of AP in nerve fibers and muscle tissue. The process of AP propagation [4, 8] includes its generation in a particular site of a conductive path, depolarization of neighboring sites to the threshold level due to local currents, and the sequential active generation of an AP at these sites. The main question in this regard is the route of the AP spread, namely, the particular plant structures through which the electric signal travels.

In lower plants, two main types of action-potential propagation may be noted. In long (several centimeters) cells of giant Characean algae, AP spreads over rows of cells connected with each other by electric contacts [54]. The process bears a fundamental resemblance to action-potential conduction along a nerve fiber. In a moss thallome, small cells are connected by plasmodesma to compose the joint electric system symplast, through which the action potential propagates [14]. This type of signal transmission is similar to the action potentials in Purkinje's fibers of the syncytium.

In higher plants, the pattern is not as straightforward. It should be mentioned first that their conducting bundles serve as a chief transmission channel [4, 8, 55, 56] but other cells are less engaged in the signal propagation. However, the structure of conducting bundles is complex and includes xylem vessels, sieve elements, and parenchyma. Because of the active character of an action potential, we can exclude the participation of inanimate xylem in its transmission. In the meantime, the possible involvement of parenchymal cells and sieve elements in AP conduction remains disputable [4, 8, 55, 58, 59].

Using the microelectrode technique, action potentials were recorded in both parenchymal cells of conducting bundles [4] and in sieve elements [8]. However, the response that is detected in some particular structure may be a result of a electrotonic transmission of a signal rather than its active propagation. There are theoretical arguments in favor of the key roles of each type of AP transmission. Thus, parenchymal cells have a high resting potential (−150 mV and lower), low excitation threshold, and their AP exhibits a large amplitude. In addition, the symplast of parenchyma is well developed, enabling a good electrical connection between these cells [4]. Nevertheless, sieve elements, despite their lower excitability, have a greater length and diameter, thus providing larger cable coefficients of these structures; therefore, they are much more effective paths for rapid and undecremented spread of an AP [60].

Previously, we theoretically analyzed the role of the symplast of parenchymal cells in AP propagation [60]. Our approach was based on a detailed model of the generation and spread of an AP in a two-dimensional system of excitable elements. With the use of empirical values of intercellular conductivity in a symplast, the analysis showed that the simulated action potential has an approximate speed of several mm/s, while the faster conduction of an AP (several cm/s or even tens of cm/s found in some locomotor plants [4]) requires greater intercellular conductivity. On the other hand, the theoretical analysis in [60] demonstrated that the increased intercellular conductivity enhances the threshold of the action potential in the system. In other words, the low excitability of sieve elements may

more likely be due to their potential effectiveness for spreading an AP than their physiology.

Therefore, the problem of the route of AP spread appears to be contradictory. On the one hand, the symplast of parenchimal cells of conducting bundles is quite excitable but less effective to conduct an action potential. On the other hand, sieve elements are more effective in AP conduction but less excitable. We can assume that the spread of an action potential takes place providing cooperation of the two paths, namely, the symplast of parenchimal cells and sieve elements. In terms of this hypothesis, stimulation initiates the generation of the primary AP and its sequential responses in symplast cells. Here, sieve elements function as the main electric channels that connect different zones of the symplast (Fig. 2). To validate this hypothesis, previously we theoretically analyzed [61] a two-dimensional system that consists of excitable elements, which were weakly electrically interconnected (simulating a symplast) and cell bundles with good electrical interconnection (simulating sieve elements). It was found that this system simultaneously imitates both the low threshold for AP generation and relatively high speed of its propagation; this supports the hypothesis of the joint participation of sieve elements and parenchmal cells in the processes of AP generation and spreading. However, the issue of AP routes in higher plants requires further experimental and theoretical investigation.

As to another electric signal type, viz., the variation potential, the aspect of its propagation mechanisms is more debatable. Historically, three hypotheses have been proposed [4]: active spreading involving local currents, spreading via a special chemical compound (a wound substance or Ricca's factor), and spreading by means of a hydraulic wave. Three important peculiarities of the propagation of the variation potential [17] are worth mentioning. These are dependency of its amplitude and spreading speed on the stimulus intensity, a decrease in its amplitude and speed with distance from an altered site, and its ability to pass through zones of physiologicvally inactive, even dead tissues. These factors rather definitely exclude the hypothesis of the active mechanism of VP propagation.

Both hydraulic and chemical hypotheses of the variation potential spread have strong and weak points. The hydraulic hypothesis is supported at least by the fact that a wave of increased tension occurs and spreads prior to the electric response [62–64]; another supporting fact is the plant's electric reaction in response to a local stress [17, 45]. Meanwhile, a hydraulic wave should spread over a plant much faster (up to the speed of sound in an aquatic medium) than the actual speed of VP spreading (mm/s or lower) [16]. This has been confirmed experimentally, for example, by the simultaneous pressure change over almost the entire stem length in the first seconds after plant experiences a burn [64] but the variation potential travels much more slowly along the stem and dampens in the course of spreading.

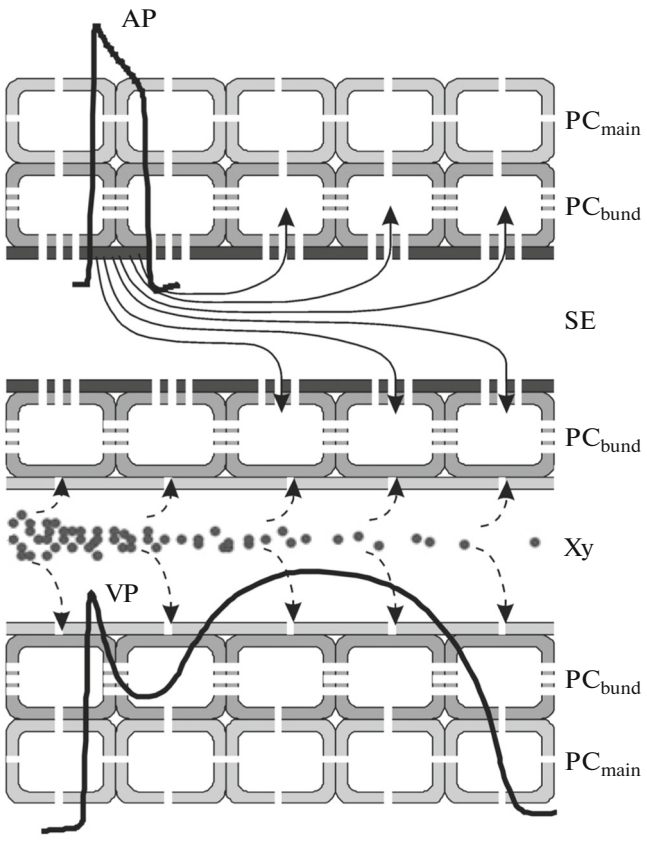

Fig. 2. Scheme of propagation processes of action potential and variation potential in higher plants: PC_{main}, parenchimal cells of main tissue; PC_{bund}, parenchimal cells of conducting bundles; SE, sieve elements; Xy, xylem. Solid arrows schematically designate local depolarizing currents, dash arrows depict influence of wound substance on cells.

The chemical hypothesis is supported by the ability of the variation potential to pass through a cut stem that is submerged in a water solution and also by the ability of plant tissue homogenates to cause reactions that resemble a VP according to some parameters [4]. However, several problems make it difficult to accept the chemical hypothesis. First, the nature of the wound substance is uncertain as yet; possible candidates are oligosaccharides from the damaged cell wall, systemin, jasmonic acid, salicylic acid, ethylene, abscisic acid, and hydrogen peroxide [16]. Second, as in the case of a hydraulic wave, the speed of VP spreading (on the order of mm/s) does not match the speeds of the molecular diffusion of various compounds (approximately mm/h) [4]. Furthermore, the initial suggestion of a transpiration stream that carries the wound substance contradicts the data of basipetal along with acropetal spreading of the VP [4].

However, the limitations of the hydraulic and chemical hypotheses may be overcome by their combination. One such combined hypothesis considers "the burst of metabolites" [65]. In this scheme, some local damage elevates the pressure, which, in turn, creates a water stream through the xylem that transfers the wound substance to intact zones of the plant. The authors of this hypothesis assume the possibility of such a transfer of the wound substance in both acropetal and basipetal directions. Nonetheless, the hypothesis faces several restrictions. First, a stable and durable stream requires the inflow of considerable volumes of water into the xylem, while the water source is uncertain. Second, such streams require long and stable pressure gradients but experiments have revealed almost simultaneous pressure changes in all parts of the plant [64]. Third, several works [49, 64] reported that the rapid movement of chemicals over the plant obeys the diffusion equation well but the diffusion coefficient exceeds the coefficient of molecular diffusion by several orders of magnitude.

These discrepancies may be eliminated by another combined hypothesis on VP propagation that we advanced previously [49, 64]. According to it (Fig. 2), the transfer of a wound substance actually exhibits a diffusion character; however, it is not molecular diffusion but the diffusion associated with convective flows of the xylem liquid. The feasibility of such diffusion is supported by calculations that show the complex (turbulent) character of water flows in the xylem [66] and by the parameters of the distribution of a radioactive label over the plant [64]. Pressure changes associated with wounding may additionally increase the speed of such diffusion [49, 64], which, in turn, further promotes the spread of the wound substance and, finally, the VP propagation. Therefore, the hypotheses of turbulent streams in the xylem fluid and related convective diffusion of the wound substance explains a large number of facts and, foremost, eliminates contradictions between the speeds of the hydraulic wave, diffusion of wound substance, and transfer of the variation potential.

All the same, it should be noted that the actual pattern of the VP propagation is relatively complex and not all facts may be explained by the proposed hypothesis; for example, although almost all the discussed hypotheses relate the VP spread with xylem of conductive bundles, some works [51] have reported a nonhomogeneous distribution of this electric signal over the leaf that probably is not linked to xylem. On the other hand, our recent (unpublished) studies revealed that parameters of VP propagation strongly depend on the degree of damage. Comparison of burning, heating, and mechanical wounding revealed not only different speeds of signal spreading but also different dependences of these speeds on the distance from the alteration site. It follows that the results cannot be fully explained by the hypothesis of convective diffusion of wound substance.

Therefore, in spite of abundant data, the problems of the propagation of the action and, especially, the variation potential remain open and require further experimental and theoretical investigations.

CONCLUSIONS

Scrutinizing the mechanisms of the generation and propagation of electric signals in higher plants revealed both universal and specific features of two reaction types, viz., the action potential and the variation potential. The generation of both potentials is based on ion-channel activation, which provides transmembrane transfer of Ca^{2+}, K^+, and Cl^- ions, and on transient changes in the activity of the electrogenic pump, viz., the H^+-ATPase of plasma membranes. The ratio of the contributions of the two systems to the formation of the reaction is different for an AP and a VP. Presumably, this ratio may vary within some one reaction type depending on the plant species, as well as the nature and the intensity of the stimulus.

Specific peculiarities may bring about parameter differences in functional responses induced by electric signals. There is evidence of relationships between the parameters (type) of an electric signal and the parameters of a functional response that is induced by it [10, 67–69]. As the functional response develops due to shifts in concentrations (primarily, of Ca^{2+} and H^+) that accompany AP and VP generation [35, 47, 70, 71], we may suppose that the dynamics in the signaling ion levels determines the differences in the development of the functional response. This means that a plant's electric signals, including variation potentials, may be not only a simple warning about a certain stimulus but also may contain information (encoded in the reaction parameters) of the nature and/or intensity of the stimulus.

ACKNOWLEDGMENTS

Analyses of the mechanisms of electric-signal generation in plants was supported by the Russian Science Foundation (project no. 14-26-00098). Analyses of the mechanisms of the electric signal propagation in plants was supported by the Ministry of Education and Science of the Russian Federation (contract no. 6.2050.2014/K).

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Translated by A. Aver'yanov