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LECTURES

Signaling Role of Action Potential in Higher Plants

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Abstract—The signaling role of action potential (AP) in higher plants is considered. The principles underlying realization of this role and the significance of AP-induced short-term effector response are discussed. The notion is put forward that the effect of propagating AP on plant cells is similar to nonspecific component of the cell functional response to external stimuli.

Key words: higher plants - action potential - signaling role

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INTRODUCTION

The functional role of action potentials (AP) in higher plant organisms attracts close attention of researchers [1–5]. This role has been studied most thoroughly for a relatively small group of so-called "motile" plants that employ AP in fast locomotory responses analogous to seismonastic movements [2, 6]. The AP seems also involved in preparing plant generative organs to fertilization [7, 8].

The function of AP is less certain for vegetative organs of higher plants, where AP are generated and propagated along the stem over long distances under the action of adverse factors [1]. Presently, it is only known that AP behave as fast distantly transmitted signals that induce short-term transient changes of many vitally important processes (respiration, photosynthesis, growth, etc.) along the route of their propagation [1, 3–5].

The following questions remain opened so far:

(1) If AP is a signal, what kind of information it transmits?

(2) What is the mechanism for accomplishing the AP signaling role?

(3) What is the meaning of AP-induced short-term effector response? What does it signify?

This article is an attempt to provide comprehensive responses to the above questions based on investigations performed in our laboratory.

Abbreviations: AP—action potential (potentials).

WHAT KIND OF SIGNALING INFORMATION IS CARRIED BY ACTION POTENTIAL?

The generation of AP in cells of vegetative organs of higher plants is preceded by the appearance of a gradual bioelectric response. This gradual response consists in plasma membrane depolarization whose properties are similar to those of the receptor potential [9, 10]. When the depolarization attains a certain critical (threshold) level, AP is generated according to the "all or none" rule [11]. The action potential appears usually as a single pulse; in rare cases several repeated pulses are generated [11, 12]. Next, AP propagates along the conducting bundles of stem beyond the area of its generation [1, 13, 14]. After reaching leaves, roots, ovary, etc., the propagating AP induces functional responses in these organs. There is no unanimous view on whether AP propagates over the root and the leaf directly or as a transformed signal or whether it acts via a series of mediators.

The generation of AP in excitable higher plant cells is chronologically linked to the early stage of stimulus action [12]. This circumstance clearly indicates the alarming (signaling) function of the pulsed bioelectric response. One may suppose that the purpose of this bioelectric response is the transmission of some information to resting tissues and organs. Meanwhile, analysis shows that the AP transmitted beyond the region of stimulation apparently cannot transfer information on the quality of stimulating external factor; it can only signalize about the onset of this factor action. Two reasons support this inference.

(1) The transmission of frequency-coded information, as it occurs in animals, would require repeated pulsed activity, which is uncharacteristic of plants. Furthermore, unlike animals, the plants have no special-

ized organ for decoding this information, analogous to the central nervous system [16].

(2) The transfer of information on stimulating factor by means of a single AP is only possible under condition that AP parameters depend on stimulus modality. Some researchers reported on the existence of such dependency [17, 18]. Particularly, the AP amplitude and propagation rate in potato plants was reportedly dependent on the nature of stimulating factors [17]. However, these data need additional explanations.

The "all or none" principle, underlying the origin of genuine AP, makes unlikely the dependency of electric pulse on stimulus specificity, provided that no variation potential (variable wave) is superimposed on the AP during injuring treatments [4].

At the same time, it is known that the cell perception of stimuli of various modalities and the subsequent transduction of the arising signals involve different transport mechanisms [19–21]. This circumstance might be reflected in the dependence of AP parameters (duration and/or amplitude) when the AP is recorded directly in the stimulation zone. However, the propagation of AP along the stem involves common conducting pathways and a unified mechanism [1], which virtually excludes the possibility that the electric pulse would depend on the physical nature of stimulus.

Thus, there is good evidence to believe that the AP transmitted along the stem of higher plants is a nonspecific bioelectric signal independent of the stimulus origin; consequently, it does not carry any stimulus-specific information.

A major part of published data supports this statement. In particular, the research of our laboratory has shown that the stems of 2-week-old pumpkin seedlings generate action potentials in response to burning (there was no variation potential) and chilling with principally similar AP parameters (amplitude, duration, and propagation velocity) [22].

Being a nonspecific bioelectric signal, the transmitted AP induces transient nonspecific functional disturbances in tissues and organs on the way of its propagation. In this case, the AP-mediated receptor–effector relationship in higher plants represents a very short chain:

Signal perception and transduction ⟶

⟶ AP ⟶

⟶ Effector (functional) response.

The receptor–effector chain in animals is more complex because it involves the central nervous system as a decoding and coordinating center [16].

OPERATION MECHANISM FOR SIGNALING ROLE OF ACTION POTENTIAL

The action potential as a biolelectric response represents the pulsed version of plasma membrane depolarization in the plant cell. Depolarization may initiate functional effects by three means [23]: (a) owing directly to the decrease in membrane potential; (b) through ionic shifts underlying depolarization; and (c) through ion flows and changes in ionic balance triggered by depolarization.

The decrease in membrane potential always releases the electromechanical tension (electrostriction) of the membrane lipid matrix, which would affect the membrane permeability and conformational mobility of protein systems residing in the membrane matrix [24]. However, since the membrane depolarization during generation and propagation of AP is transient and reversible, one can hardly expect any functional significance of these changes.

A more probable alternative is that the AP transmission initiates various nonspecific functional changes (e.g., enhancement of respiration, suppression of photosynthesis, biosynthesis of stress hormones, etc. [4]) owing to intracellular concentration changes resulting from ion flows involved in AP generation (Ca^{2+}, Cl^-, K^+, and H^+ fluxes [1, 25, 26]). Two circumstances should be taken into account.

The first circumstance is that physiological activity of ion species involved in AP generation is very high. It is known that Ca^{2+} is one of the principal intracellular messengers [27–29]. During AP generation and propagation, Ca^{2+} enters the cytoplasm through voltage-gated Ca^{2+} channels of the plasma membrane and is released from intracellular stores [26, 30–32]. These fluxes give rise to the Ca^{2+} signal [27–29]. Within the framework of this signaling, Ca^{2+} ions bind to a regulatory protein calmodulin, thus acquiring the ability to activate a series of enzymes, e.g., protein kinases that phosphorylate various intracellular and membrane proteins and modulate their functional activity.

A factor of no less importance is the close association of the calcium signal during AP generation and propagation with other forms of intracellular signaling, the proton signaling in particular [26].

The proton signal is due to the fact that the AP generation in higher plant cells is coupled to the activity of the plasma membrane electrogenic H^+ pump (H^+-ATPase). This pump is temporally inactivated during the initial stage of cell excitation, which results in the transient alkalization of the apoplast and, supposedly, acidification of the cytoplasm [25, 26]. The temporal acidification of the cytoplasm during AP generation initiates the proton signaling system, which in turn is implicated in the control of cell metabolism and gene expression [27, 33, 34].

The second important circumstance is that changes in ionic concentrations during AP generation and propagation are rather large for some ion species [1, 30, 35]. For example, K^+ concentration in parenchymal cells in conducting bundles of the pumpkin stem decreases during a single AP by 30 mM [30], whereas the K^+ concentration in nerve cells of animals decreases by only 1 μM

Table 1. Comparative characterization of AP signals in animals and higher plants

AP in animals	AP in "usual" higher plants
1. Rhythmical repeated pulses combined in groups; appearance of single AP seems to be an artifact rather than the norm	1. Usually appear as a single AP; rarely, in groups of few repeated pulses
2. AP arise in specialized receptor cells	2. AP arise in cells of surface tissues exposed to stimulation
3. AP generation is not associated with large ionic shifts and metabolic changes	3. AP generation is accompanied by large ionic shifts and changes in metabolism
4. AP carry frequency-encoded information on the stimulus	4. AP do not contain information on the stimulus
5. AP are coordinated by the central nervous system	5. "Uncontrolled" signals
6. AP induce specific effector response in particular parts of the organism	6. AP induce nonspecific effector response throughout the pathway of AP transmission over the organism
7. AP is a "pure" signal (i.e., it performs a signaling role only)	7. AP is a systemic signal that represents a part of the effector response

after one pulse [15]. The reason behind these large changes is that ion flux densities during AP in higher plant cells are similar to those in animals, whereas the pulse duration is several orders of magnitude longer [1]. A considerable efflux of K^+ from the cells where AP are generated and propagated under injuring treatments might have a protective role related to modulation of cell metabolism, enzyme activities, turgor, etc. [36, 37].

By considering all these circumstances, we conclude that the Ca^{2+} and H^+ influxes into the cytoplasm and the efflux of K^+ during cell excitation may be of key significance for the formation of AP-induced effector response.

WHAT IS THE MEANING OF ACTION POTENTIAL-INDUCED EFFECTOR RESPONSE?

Owing to a short length of receptor–effector chain in higher plants, the requirements imposed upon AP as a mediator element are inevitably different from those imposed on the nerve pulse (Table 1).

The AP in plants usually represents a single systemic signal affecting all organs and tissues where it propagates. Considering large-scale ionic and metabolic shifts during AP generation and propagation in plants [1, 25, 38], AP can be regarded not merely as a signal linking stimulus reception and the effector response but also as a part of the effector response. At the same time, as noted above, the AP transmitted along the plant stem does not carry information on the stimulus origin, but it gives a signal to resting tissues and organs about the onset of adverse conditions in some region. This information is linked to the very fact of AP appearance and propagation.

In the absence of the coordinating center analogous to the central nervous systems of animals, AP provides for the direct connection between reception and the effector response. The propagating AP can effectively perform the signaling role because, similarly to the excitation stimulus, it induces changes analogous to nonspecific component of the functional response in the region of immediate excitation.

In order to substantiate the above statement, let us consider Table 2, where the left column lists the most significant nonspecific changes characteristic of higher plant cells under stress, while the right column contains data on the development of similar changes during AP generation and propagation.

Table 2 shows that the correlation of the above changes has been already found for most items listed. This refers to the earliest nonspecific changes, including membrane depolarization, permeability changes, and ionic shifts during AP, and is also valid with respect to functional rearrangements comprising major metabolic and physiological processes, gene expression, biosynthesis of stress hormones, etc.

On the whole, Table 2 suggests that the AP electrical signals in higher plants behave similarly to the excitation agent and induce the condition of short-term functional perturbation (stress) away from the excitation region. However, it is not excluded that the observed similarity is only phenomenological, because the mechanisms underlying unidirectional effects of AP and some stressful factors on physiological and metabolic processes in plant cells can differ substantially [55]. The durations of these effector responses also dif-

Table 2. Involvement of AP in initiation of stress in higher plants

The most significant nonspecific changes in stressed plant cells [39, 40]	Initiation of analogous nonspecific changes during AP generation and propagation
1. Changes in ionic permeability of cell membranes	1. Considerable changes of plasma membrane permeability during AP to Ca^{2+}, Cl^-, and K^+ [1, 41]
2. Plasma membrane depolarization	2. Representative AP in higher plants is generated and transmitted as a pulse-like depolarization with an amplitude of several tens of millivolt [1, 4]
3. The increase in cytoplasmic Ca^{2+} concentration	3. During AP generation and propagation, Ca^{2+} enters the cytoplasm of higher plant cells from the external medium through the plasma membrane channels and is released from intracellular stores [26, 31, 32]
4. Acidification of the cytoplasm	4. During AP generation in plant cells, the cytoplasmic pH decreases and the external medium is alkalized [26, 42], which is supposedly caused by transient suppression of electrogenic plasma membrane H^+ pump (H^+-ATPase) during excitation [25]
5. Multiphase development of the stress-induced response	5. Multiphase changes were observed for root absorption after arrival of AP to the root from the leaves [43], for ATP content in the phloem exudate after AP transmission along the stem [38], etc. The AP was shown to control multiphase changes in resting potential in the region of stress treatment [44]
6. The increase in free radical content	6. Propagation of AP over the plant is accompanied by generation of free radicals [45]
7. Enhanced catabolism of lipids and biopolymers	7. No data
8. Enhancement of respiration	8. Respiration rate increases under the influence of AP or AP-comprising electric signals* [46, 47]
9. Inhibition of photosynthesis	9. Photosynthetic parameters undergo transient changes under the influence of AP or AP-comprising electric signals*, which indicates temporal suppression of photosynthesis [48, 49]
10. Increase in ABA and jasmonic acid content	10. Induction of ABA and jasmonic acid under the influence of AP or AP-comprising electric signals [50, 51]
11. Ethylene production	11. AP stimulates ethylene production [52]
12. Suppression of cell division and growth	12. Stem elongation is retarded after generation and propagation of AP [53]
13. Synthesis of stress (shock) proteins	13. No data
14. Accelerated synthesis of cell wall components (lignin, cutin, callose, etc.)	14. No data
15. Proline accumulation	15. No data
16. Accumulation of organic polyamine	16. No data
17. Action of biostressors (bacteria, fungi, viruses, and insects) results in production of various pathogen-induced proteins, chitinases, and proteinase inhibitors	17. The AP or AP-comprising electric signals* induce the expression of proteinase inhibitors and calmodulin genes [51, 52]

Note: * Electric signals generated and propagated under the treatments of injuring intensities have usually complex structure and include AP in combination with a slower wave of variable shape [54].

fer: unlike the sustained stress, the AP-induced response is a short-term reversible transient [4].

It is known that the development of stress in plants eventually elevates plant resistance to stress factors, provided that reliability resources are unexhausted [56]. Therefore, it is natural to expect that the plant may acquire to some extent the condition of elevated resistance under the influence of AP. Our studies [57, 58] provided convincing evidence that AP propagation rapidly elevates nonspecific resistance of plant tissues outside the stimulation area (in the regions affected by propagating AP) for 12–60 min after the pulse transmission. This phenomenon was designated as the AP-induced preadaptation [57]. The resistance of plant materials was assessed by means of electrophysiological method in combination with tissue freezing [57] and from the delayed fluorescence measurements in photosynthetic tissues under unified conditions [58].

The development of preadaptation state is thought to facilitate the survival of higher plants under unfavorable conditions in the period before the adaptive changes are mobilized [4]. Therefore, this phenomenon can be considered as an important aspect of plant "intelligent" behavior [59]. The extent of AP-induced preadaptation in plants is apparently regulated through the increase in the number of generated and transmitted signals (from one to several), as it was observed, for example, under combined action of several different stress factors [60].

It should be noted in conclusion that the presented view of AP as a stress (excitatory) signal and the AP-induced phenomenon of preadaptation provide satisfactory explanation for numerous reports on fast long-distance transmission of not only "stress signals" but also "hardening signals" [61–64].

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REFERENCES

1. Opritov, V.A., Pyatygin, S.S., and Retivin, V.G., *Bioelektrogenez u vysshikh rastenii* (Bioelectrogenesis in Higher Plants), Moscow: Nauka, 1991.
2. Sibaoka, T., Rapid Plant Movements Triggered by Action Potentials, *Bot. Mag.* (Tokyo), 1991, vol. 104, pp. 73–95.
3. Thain, J.F. and Wildon, D.C., Electrical Signalling in Plants, *Membranes: Specialized Functions in Plants*, Smallwood, M., Knox, J.R., and Bowles, D.J., Eds., Oxford: BIOS Sci. Publ., 1996, pp. 301–317.
4. Pyatygin, S.S., Electrogenesis of Plant Cells under Stress Conditions, *Usp. Sovrem. Biol.*, 2003, vol. 123, pp. 552–562.
5. Davies, E., New Functions for Electrical Signals in Plants, *New Phytol.*, 2004, vol. 161, pp. 607–610.
6. Wejnar, R., *Bewegungen der Pflanzen*, Berlin: Urania-Verlag, 1982.
7. Sinyukhin, A.M. and Britikov, E.A., Action Potentials in the Reproductive System of Plants, *Nature*, 1967, vol. 215, pp. 1278–1280.
8. Dukhovnyi, A.I., *Elektrofiziologiya opyleniya u vysshikh rastenii (na primere kukuruzy)* (Electrophysiology of Pollination in Higher Plants as Exemplified by Maize), Chisinau: Shtiintsa, 1973.
9. Shimmen, T., Involvement of Receptor Potentials and Action Potentials in Mechanoperception in Plants, *Aust. J. Plant Physiol.*, 2001, vol. 28, pp. 567–576.
10. Opritov, V.A., Lobov, S.A., Pyatygin, S.S., and Mysyagin, S.A., Analysis of Possible Involvement of Local Bioelectric Responses in Chilling Perception by Higher Plants Exemplified by *Cucurbita pepo, Russ. J. Plant Physiol.*, 2005, vol. 52, pp. 801–808.
11. Pyatygin, S.S. and Opritov, V.A., Effect of Temperature on Action Potential Generation by Excitable Higher Plant Cells, *Biofizika*, 1990, vol. 35, pp. 444–449.
12. Pyatygin, S.S., Opritov, V.A., and Khudyakov, V.A., Subthreshold Changes in Excitable Membranes of *Cucurbita pepo* L. Stem Cells during Cooling-Induced Action-Potential Generation, *Planta*, 1992, vol. 186, pp. 161–165.
13. Eschrich, W., Fromm, J., and Evert, R.F., Transmission of Electric Signals in Sieve Tubes of *Zucchini* Plants, *Bot. Acta*, 1988, vol. 101, pp. 327–331.
14. Rhodes, J.D., Thain, J.F., and Wildon, D.C., The Pathway for Systemic Electrical Signal Conduction in the Wounded Tomato Plants, *Planta*, 1996, vol. 200, pp. 50–57.
15. Yost, H., *Cellular Physiology*, New Jersey: Prentice-Hall, 1972.
16. Smit, K.Yu.M., *Biologiya sensornykh sistem* (Biology of Sensor Systems), Moscow: BINOM, Laboratoriya znanii, 2005.
17. Volkov, A.G. and Haack, R.A., Bioelectrochemical Signals in Potato Plants, *Sov. Plant Physiol.*, 1995, vol. 42, pp. 23–29.
18. Volkov, A.G. and Haack, R.A., Insect Induced Bioelectrochemical Signals in Potato Plants, *Bioelectrochem. Bioenerg.*, 1995, vol. 35, pp. 55–60.
19. Fasano, J.M., Massa, G.D., and Gilroy, S., Ionic Signaling in Plant Responses to Gravity and Touch, *J. Plant Growth Regul.*, 2002, vol. 21, pp. 71–88.
20. Jaffe, M.J., Leopold, A.C., and Staples, R.C., Thigmo Responses in Plants and Fungi, *Am. J. Bot.*, 2002, vol. 89, pp. 375–382.
21. Pyatygin, S.S., Role of Plasma Membrane in Cold Action Perception in Plant Cells, *Biol. Membr.* (Moscow), 2004, vol. 21, pp. 442–449.
22. Pyatygin, S.S., Rhythmical Electric Activity in Pumpkin Seedlings under Damaging and Moderate Temperature Stimuli, *Fermenty, iony i bioelektrogenez u rastenii* (Enzymes, Ions, and Bioelectrogenesis in Plants), Anisimov, A.A. and Opritov, V.A., Eds., Gorky: Gork. Gos. Univ., 1982.
23. Pyatygin, S.S., Vodeneev, V.A., and Opritov, V.A., Depolarization of the Plasma Membrane as a Universal Primary Bioelectric Response of Plant Cells to Various Factors, *Usp. Sovrem. Biol.*, 2006, vol. 126, pp. 493–502.

24. Pyatygin, S.S. and Opritov, V.A., Effect of Membrane Potential on the Lipid Matrix Phase State in the Plasma Membrane of Intact Plant Cells under Moderate Above-Zero Temperatures, *Biofizika*, 1993, vol. 38, pp. 175–178.
25. Pyatygin, S.S., Vodeneev, V.A., and Opritov, V.A., Coupling of Action Potential Generation and Metabolism in Plant Cells: Current View on the Problem, *Usp. Sovrem. Biol.*, 2005, vol. 125, pp. 520–528.
26. Vodeneev, V.A., Opritov, V.A., and Pyatygin, S.S., Reversible Changes of Extracellular pH during Action Potential Generation in a Higher Plant *Cucurbita pepo, Russ. J. Plant Physiol.*, 2006, vol. 53, pp. 481–487.
27. Tarchevsky, I.A., *Signal'nye sistemy kletok rastenii* (Signal Transduction Pathways in Plant Cells), Moscow: Nauka, 2002.
28. White, J.P. and Broadley, M.R., Calcium in Plants, *Ann. Bot.*, 2003, vol. 92, pp. 487–511.
29. Plieth, C., Calcium: Just Another Regulator in the Machinery of Life? *Ann. Bot.*, 2005, vol. 96, pp. 1–8.
30. Opritov, V.A., Retivin, V.G., and Pyatygin, S.S., Nature of Action Potential in Higher Plants, *Elektrofiziologicheskie metody v izuchenii funktsional'nogo sostoyaniya rastenii* (Electrophysiological Methods for Investigation of Plant Functional Status), Puponin, A.I., Ed., Moscow: Timiryazev. S.-kh. Acad., 1988, pp. 14–22.
31. Krol, E., Dziubinska, H., and Trebacz, K., Low-Temperature Induced Transmembrane Potential Changes in the Liverwort *Conocephalum conicum, Plant Cell Physiol.*, 2003, vol. 44, pp. 527–533.
32. Krol, E., Dziubinska, H., Stolarz, M., and Trebacz, K., Effects of Ion Channel Inhibitors on Cold- and Electrically-Induced Action Potentials in *Dionaea muscipula, Biol. Plant.*, 2006, vol. 50, pp. 411–416.
33. Wilkinson, S., pH as a Stress Signal, *Plant Growth Regul.*, 1999, vol. 29, pp. 87–99.
34. Roos, W., Viehweger, K., Dordschbal, B., Schumann, B., Evers, S., Steighardt, J., and Schwartze, W., Intracellular pH Signals in the Induction of Secondary Pathways – The Case of *Eschscholzia californica, J. Plant Physiol.*, 2006, vol. 163, pp. 369–381.
35. Fromm, J. and Spanswick, R., Characteristics of Action Potentials in Willow (*Salix viminalis* L.), *J. Exp. Bot.*, 1993, vol. 44, pp. 1119–1125.
36. Melekhov, E.I. and Anev, V.N., Reversible K^+ Efflux from the Cell as a Defense Response to Adverse Effects, *Zh. Obshch. Biol.*, 1991, vol. 52, pp. 14–26.
37. Melekhov, E.I. and Anev, V.N., Mechanisms of Cell Defense Responses Coupling with K^+ Efflux, *Usp. Sovrem. Biol.*, 1992, vol. 112, pp. 18–28.
38. Retivin, V.G., Opritov, V.A., Abramova, N.N., Lobov, S.A., and Fedulina, S.B., ATP Level in the Phloem Exudate of Higher Plant Shoot after Propagation of Electric Responses to the Burning or Cooling, *Vestn. Nizhegorod. Univ. im. N.I. Lobachevskogo, Ser. Biol.*, 1999, no. 1, pp. 124–131.
39. Tarchevsky, I.A., *Metabolizm rastenii pri stresse* (Plant Metabolism under Stress), Kazan: Fen, 2001.
40. Lukatkin, A.S., *Kholodovoe povrezhdenie teplolyubivykh rastenii i okislitel'nyi stress* (Cold Damage to Heat-Loving Plants and Oxidative Stress), Saransk: Mordovsk. Univ., 2002.
41. Trebacz, K., Simonis, W., and Schönknecht, G., Cytoplasmic Ca^{2+}, K^+, Cl^-, and NO_3^- Activities in the Liverwort *Conocephalum conicum* L. at Rest and during Action Potential, *Plant Physiol.*, 1994, vol. 106, pp. 1073–1084.
42. Bulychev, A.A. and Remish, D., Transient Inhibition of the H^+-Pump in *Anthoceros* Plasmalemma after Light Flash of Second Duration, *Sov. Plant Physiol.*, 1991, vol. 38, pp. 499–505.
43. Opritov, V.A., Krauz, V.O., and Treushnikov, V.M., The Role of Electric Responses of Excitation in Functional Relations between Shoots and Roots after Seedling Apex Stimulation by External Cues, *Sov. Plant Physiol.*, 1972, vol. 19, pp. 961–967.
44. Opritov, V.A., Pyatygin, S.S., and Krauz, V.O., Analysis of the Role of Electric Activity in Higher Plant Cell and Development of Adaptive Syndrome under Cooling, *Russ. Plant Physiol.*, 1993, vol. 40, pp. 619–626.
45. Opritov, V.A., Kalinin, V.A., and Yarchenkova, I.M., Participation of Free Radicals in the Mechanism of Action Potential Propagation in Cells of Conducting System in Higher Plants, *Sov. Plant Physiol.*, 1974, vol. 21, pp. 545–553.
46. Dziubinska, H., Trebacz, K., and Zawadzki, T., The Effect of Excitation on the Rate of Respiration in the Liverwort *Conocephalum conicum, Physiol. Plant.*, 1989, vol. 75, pp. 417–423.
47. Filek, M. and Koscielniak, J., 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.*, 1997, vol. 123, pp. 39–46.
48. Fromm, J. and Eschrich, W., Electric Signals Released from Roots of Willow (*Salix viminalis* L.) Change Transpiration and Photosynthesis, *J. Plant Physiol.*, 1993, vol. 141, pp. 673–680.
49. Koziolek, C., Grams, T.E.E., Schreiber, U., Matyssek, R., and Fromm, J., Transient Knockout of Photosynthesis Mediated by Electrical Signals, *New Phytol.*, 2004, vol. 161, pp. 715–722.
50. Roberts, K., Potential Awareness of Plants, *Nature*, 1992, vol. 360, pp. 14–15.
51. Fisahn, J., Herde, O., Willmitzer, L., and Pena-Cortes, H., Analysis of the Transient Increase in Cytosolic *Anthoceros* during the Action Potential of Higher Plants with High Temporal Resolution: Requirement of Ca^{2+} Transients for Induction of Jasmonic Acid Biosynthesis and PIN II Gene Expression, *Plant Cell Physiol.*, 2004, vol. 45, pp. 456–459.
52. Dziubinska, H., Filek, M., Koscielniak, J., and Trebacz, K., Variation and Action Potentials Evoked by Thermal Stimuli Accompany Enhancement of Ethylene Emission in Distant Non-Stimulated Leaves of *Vicia faba minor* Seedlings, *J. Plant Physiol.*, 2003, vol. 160, pp. 1203–1210.
53. Shiina, T. and Tazawa, M., Action Potential in *Luffa cylindrica* and Its Effects on Elongation Growth, *Plant Cell Physiol.*, 1986, vol. 27, pp. 1081–1089.
54. Vian, A., Henry-Vian, C., Schantz, R., Ledoigt, G., Frachisse, J.-M., Desbiez, M.-O., and Julien, J.-L., Is Membrane Potential Involved in Calmodulin Gene Expres-

sion after External Stimulation in Plants? *FEBS Lett.*, 1996, vol. 380, pp. 93–96.

55. Bulychev, A.A. and Kamzolkina, N.A., Effect of Action Potential on Photosynthesis and Spatially Distributed H^+ Fluxes in Cells and Chloroplasts of *Chara corallina, Russ. J. Plant Physiol.*, 2006, vol. 53, pp. 1–9.
56. Veselova, T.V., Veselovskii, V.A., and Chernavskii, D.S., *Stress u rastenii (Biofizicheskii podkhod)* (Stress in Plants, Biophysical Approach), Moscow: Mosk. Gos. Univ., 1993.
57. Retivin, V.G., Opritov, V.A., and Fedulina, S.B., Generation of Action Potential Induces Preadaptation of *Cucurbita pepo* L. Stem Tissues to Freezing Injury, *Russ. J. Plant Physiol.*, 1997, vol. 44, pp. 432–442.
58. Retivin, V.G., Opritov, V.A., Lobov, S.A., Tarakanov, S.A., and Khudyakov, V.A., Changes in the Resistance of Photosynthesizing Cotyledon Cells of Pumpkin Seedlings to Cooling and Heating, as Induced by the Stimulation of the Root System with KCl Solution, *Russ. J. Plant Physiol.*, 1999, vol. 46, pp. 689–696.
59. Trewavas, A., Green Plants as Intelligent Organisms, *Trends Plant Sci.*, 2005, vol. 10, pp. 413–419.
60. Pyatygin, S.S., Opritov, V.A., Abramova, N.N., and Vodeneev, V.A., Primary Bioelectric Response of Higher Plant Cells to the Combined Action of Stress Factors, *Russ. J. Plant Physiol.*, 1999, vol. 46, pp. 530–536.
61. Akimova, T.V., Balagurova, N.I., and Titov, A.F., Possibility of Heat Hardening "Signal" Transduction in Plants, *Sov. Plant Physiol.*, 1991, vol. 38, pp. 1197–1202.
62. Filek, M. and Koscielniak, J., The Effect of Chilling Maize Shoots and Roots on the Electric Potential, Composition of Fatty Acids and the ATPase Activity in the Non-Chilled Organs of Seedlings, *J. Agric. Crop Sci.*, 1996, vol. 117, pp. 261–267.
63. Balagurova, N.I., Akimova, T.V., and Titov, A.F., The Effect of Local Cooling of Cucumber and Wheat Seedlings on Various Kinds of Stress Resistance of Their Leaves and Roots, *Russ. J. Plant Physiol.*, 2001, vol. 48, pp. 95–99.
64. Capone, R., Tiwari, B.S., and Levine, A., Rapid Transmission of Oxidative and Nitrosative Stress Signals from Roots to Shoots in *Arabidopsis, Plant Physiol. Biochem.*, 2004, vol. 42, pp. 425–428.