===== REVIEW =====

Changes in Activity of the Plasma Membrane H+-ATPase as a Link Between Formation of Electrical Signals and Induction of Photosynthetic Responses in Higher Plants

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Abstract—Action of numerous adverse environmental factors on higher plants is spatially-heterogenous; it means that induction of a systemic adaptive response requires generation and transmission of the stress signals. Electrical signals (ESs) induced by local action of stressors include action potential, variation potential, and system potential and they participate in formation of fast physiological changes at the level of a whole plant, including photosynthetic responses. Generation of these ESs is accompanied by the changes in activity of H+-ATPase, which is the main system of electrogenic proton transport across the plasma membrane. Literature data show that the changes in H+-ATPase activity and related changes in intra- and extracellular pH play a key role in the ES-induced inactivation of photosynthesis in non-irritated parts of plants. This inactivation is caused by both suppression of CO_2 influx into mesophyll cells in leaves, which can be induced by the apoplast alkalization and, probably, cytoplasm acidification, and direct influence of acidification of stroma and lumen of chloroplasts on light and, probably, dark photosynthetic reactions. The ES-induced inactivation of photosynthesis results in the increasing tolerance of photosynthetic machinery to the action of adverse factors and probability of the plant survival.

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INTRODUCTION

Plants exist in unstable environment and could be subjected to the action of adverse factors with many of them affecting a plant in a spatially-heterogenous manner (such as excessive illumination, high and low temperatures, water deficit, biotic damage, and many others). That is why plants must have a system of 'long-distance' stress signals, which appear in the zone of the local effect and are transmitted into the intact parts of the plant organism causing adaptive physiological changes. Electrical signals (ESs) comprise an important group of stress signals affecting a wide range of physiological processes and lead to the increase of tolerance of the pant to adverse factors [1-7].

Abbreviations: AP, action potential; ES, electric signal; ROS, reactive oxygen species; SP, system potential; VP, variation potential.

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ESs are reversible changes of electrical potential differences on a plasma membrane that are capable of propagating within the plant. The main approach of measuring such electrical signals is the use of non-polarizing electrodes [1, 2]. In this case, when the measuring electrodes are placed extracellularly they contact with different parts of the plant surface, which allows more effectively to investigate propagation of the signals; in the case of intracellular placement of electrodes, the measuring electrode is introduced inside the plant cell, which allows to investigate parameters of ESs and their ionic mechanisms in more details.

It is known that ESs could stimulate in higher plants expression of protective genes (such as *pin1*, *pin2*, and *vsp2* participating in protection against insects [8, 9]), production of stress-related phytohormones (for example, abscisic and jasmonic acid [10-12]), activation of respiration [13-15], increase of ATP content in leaves [16], as well as stop of assimilate movement in phloem [17-19], changes in transpiration [20, 21],

slowing down growth processes [22], and many other responses. Role of ESs in the development of such physiological responses is conformed by the association of their parameters with characteristics of electrical signals [2, 6]. This role has been also demonstrated by revealing induction of the physiological responses during imitation of ES generation (treatment with inhibitors of proton transport or protonophores) and by suppression of the response development during blocking of the signal transduction by subjecting the stem to local effect of low temperatures or sodium azide [2, 6, 13, 23]. In particular, it was shown that expression of the protective genes occurs only in those Arabidopsis leaves where prolonged ESs are generated or those subjected to direct effects of electrical current [9].

Photosynthetic processes should be mentioned as a separate 'target' of ESs, because it is known that electrical signals could cause either short-term (5-10 min) or long-term (tens of minutes, likely hours) inactivation of photosynthesis [6, 7, 23]. Such inactivation is manifested by decrease of photosynthetic assimilation of CO_2 [10, 11, 16, 20, 24], decrease of quantum yields of the photosystems I and II [25-27] and of non-cyclic electron flow [28], and by the increase of non-photochemical quenching of the chlorophyll fluorescence [14, 27-29] (in particular of the energy-dependent component [30]), as well as increase of the cyclic electron flow around the photosystem I [28].

The presumed result of the ES-induced physiological changes is increase of the plant organism tolerance to adverse environmental factors [6, 7, 23, 31]. In particular, it was shown that propagation of ESs decreases damage of cell membranes and photosynthetic apparatus under excessive illumination [32, 33], decreases negative effects of heat [33-39] and cold [34] on photosynthetic processes, as well as increases resistance at the level of whole plant to low [40] and high [36] temperatures.

Hence, ESs play an important role in the systemic adaptation of higher plants to unstable environmental conditions [6, 7, 31]. Photosynthetic responses, development of which important for formation of the ES-induced increase of resistance of plants to adverse conditions, provide significant contribution to this adaptation [23]. That is why the main goal of this review is analysis of the pathways involved in formation of such responses for different types of electrical signals, which are based on their ionic mechanisms.

TYPES OF ELECTRICAL SIGNALS IN PLANTS AND ROLE OF THE PLASMA MEMBRANE H$^+$-ATPase IN THEIR FORMATION

Action potential (AP), variation potential (VP), and system potential (SP) are the main types of ESs in higher plants [5-7].

AP is a relatively short impulse reaction (tens of seconds) appearing during local action of damaging stressors (such as cooling by several degrees) that involves two phases (depolarization and repolarization) [1, 6, 7] (Fig. 1). In higher plants this signal is characterized by the existence of potential generation threshold, all-or-none type of signal initiation, prolonged refractory period (hours), and ability for active transmission along the sieve elements and/or symplast parenchymal cells of the plant vascular bundles via local electrical currents in plasmodesmata.

It must be mentioned that the mechanisms of AP generation are similar in higher plants and in Charophyte algae, therefore ionic mechanism of AP and association of its generation with the changes in activity of proton transport were first demonstrated for Charophyte algae [41-44] and later confirmed in higher plants. The factor initiating generation of AP is depolarization of the membrane potential to the threshold level resulting in activation of the voltage-gated Ca^{2+}-channels in plasma membrane and influx of calcium ions into the cell [1, 45-47]. Significant increase of Ca^{2+} concentration in cytoplasm [47] results in activation of anion channels and efflux of Cl^- ions from the cell [45], as well as in temporary inactivation of the plasma membrane H$^+$-ATPase [46]; these both processes lead to formation of the depolarization phase of AP. Depolarization results in activation of the outwardly-rectifying K^+-channels that mediate efflux of potassium ions from cytoplasm into extracellular space [47]. Significant depolarization also leads to the closing of Ca^{2+}-channels, decrease of calcium ion concentration in cytoplasm, and, as a result, decrease in activity of anion channels and re-activation of H$^+$-ATPase [47]. These processes result in formation of the repolarization phase and return of the membrane potential to the initial level.

Variation potential (VP) appears under the action of damaging stressors (including burn, extreme heat, mechanical damage); it has long duration (up to tens of minutes and more) and complex shape [6, 23, 48] including two components: prolonged depolarization wave and AP-like spikes, which are not always observed (Fig. 2). The AP-like spikes are typical action potentials induced by the positive shift of membrane potential in the course of formation of the long-term depolarization wave, which have the same ionic mechanisms as AP [48]; at the same time, the long-term wave is the main component of VP. One of the important features of VP (predominantly of the long-term depolarization wave) is decrease of its transmission rate [49, 50] and/or its amplitude [16, 29, 50] with the increase of the distance from the zone of damage.

VP comprises a local electrical response to transmission of a signal with non-electrical nature [48], which could be either hydraulic or chemical. The hydraulic hypothesis [22, 48, 51, 52] suggests that during local
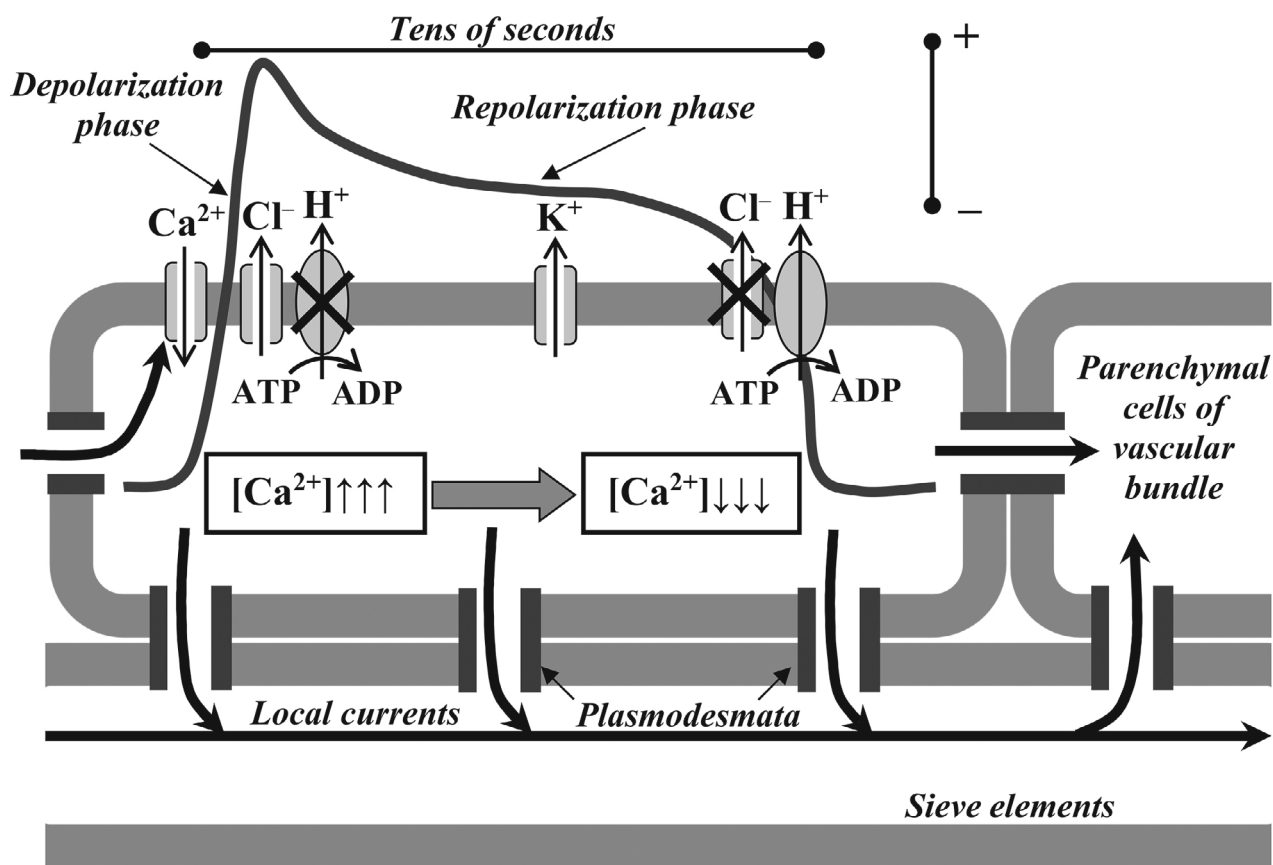
Fig. 1. Action potential in higher plants and schematic representation of the mechanisms of its generation and transmission along the vascular bundles in plants.

damages in the zone of the stressor action a region of increased pressure is formed that induces transmission of a fading hydraulic wave in the plant, which, in turn, causes activation of the mechanosensitive Ca^{2+}-channels followed by the development of VP [44]. Experimental [51] and theoretical [53] studies show that the decrease of amplitude of the hydraulic wave results in the increase of the lag-phase before the changes of electrical potential, and, thus, causes reduction of the apparent rate of VP transmission with the increase of the distance from the zone of the stressor action. Low amplitude of the hydraulic wave does not cause formation of VP.

Alternative hypothesis suggests that the release of a specific chemical compound ('wound substance') occurs in the damaged zone, diffusion of which causes activation of the ligand-dependent Ca^{2+}-channels and development of VP [48]; low intensity of such signal does not induce formation of the variation potential. H_2O_2 is often assumed as such wound substance [54-56]; however, participation of other compounds (such as systemin [57] or glutamate [58]) cannot be ruled out. The key problem of the chemical hypothesis is the low speed of molecular diffusion of the wound substance [48]. There are several approaches allowing to overcome this limitation. Firstly, according to the Malone hypothesis [59],

which has been theoretically tested in a number of mathematical models [60, 61], local increase of pressure in the zone of damage could result in emergence of additional flows of water along the xylem, which could bring the wound substance to undamaged part of the plant. Secondly, the possibility of accelerated spread of the chemical agent within a plant, which likely is associated with the enhancement of convective (turbulent) diffusion in a fluid flow in the xylem, has been previously shown in our studies [49, 62]. It must be mentioned that despite the relatively low rates of fluid flow in the xylem vessels, turbulent flows could potentially appear as a result of periodic constriction of their diameter [62]. And, thirdly, according to the hypothesis suggested by Mittler et al. [54] and developed further in the later studies [55, 56, 63], secondary generation of H_2O_2 (based on activation of Ca^{2+}-channels, increase of Ca^{2+} concentration that causes activation of NADPH oxidases RbohD in the plasma membrane, which, in turn, produce reactive oxygen species (ROS)) could occur during propagation of the chemical signal; this secondary generation could accelerate transmission of the chemical signal in the plant. Both experimental data [63] demonstrating propagation of the ROS wave (increase of their concentration) and suppression of this wave under the action
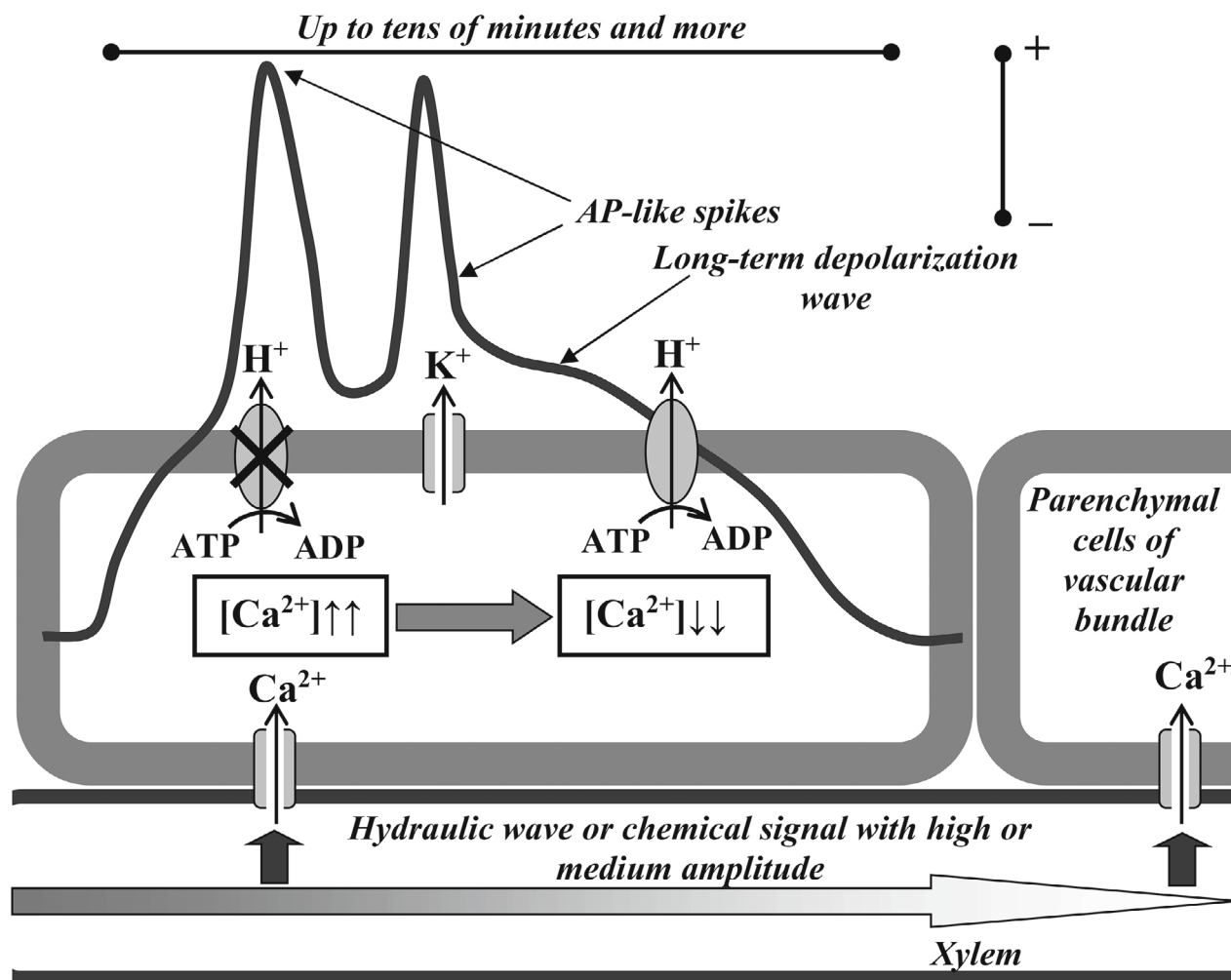
Fig. 2. Variation potential in higher plants and schematic presentation of the suggested mechanisms of its generation and transmission along the vascular bundles in plants. Scheme of formation of long-term depolarization wave associated with high or medium increase of Ca^{2+} concentration in cytoplasm is shown. Mechanisms of AP-like spikes are similar to AP mechanisms (see Fig. 1) and are not shown in this figure.

of inhibitor of RbohD oxidases and the results of mathematical modeling support this hypothesis.

It is generally accepted that propagation of chemical signal or of hydraulic wave results in the long-term activation of the ligand-dependent or mechanosensitive Ca^{2+}-channel in the plasma membrane, and, respectively, influx of calcium ions into the cell [48]. Moderate (or large) and long-term increase of Ca^{2+} concentration in cytoplasm (500-600 nM and above [49]) causes inactivation of the H$^+$-ATPase [64] and formation of the long-term depolarization wave. In the background of this wave, the membrane potential could reach the threshold level and activate the voltage-gated Ca^{2+}-channels, thus forming AP-like spikes, mechanism of which is similar to the AP mechanism [48, 49].

System potential (SP), which comprises a propagating wave of hyperpolarization (Fig. 3), is the least investigated type of electrical signals in plants [6]. It is known that SP could appear in response to the action of a wide spectrum of stressors including inorganic salts, moderate and high heat, burn, mechanical damage, and attacks of insects [9, 65-71]. In the process, the shape and duration of SP could vary significantly depending on the type of stressor, plant species, and distance from the zone of damage [9, 65-71]. It must be mentioned that SP could be closely associated with VP, because (i) a number of stressors cause generation of VP close to the damage zone, while SP appears at a larger distance from it [9, 67, 69-71]; (ii) local burn causes VP in the plants watered regularly, but could cause development of SP under severe water deficit [69]; (iii) stressors could cause VP during first exposure, and the repeated exposure causes SP [66]; (iv) depending on location of the zone of stressor action in the plant the same stressor could cause either VP or SP [65].

It is generally considered that activation of the H$^+$-ATPase in plasma membrane is the main mechanism of SP generation [66], which has been confirmed by suppression of the signal during prior inhibition of this transporter (sodium orthovanadate) and by induction
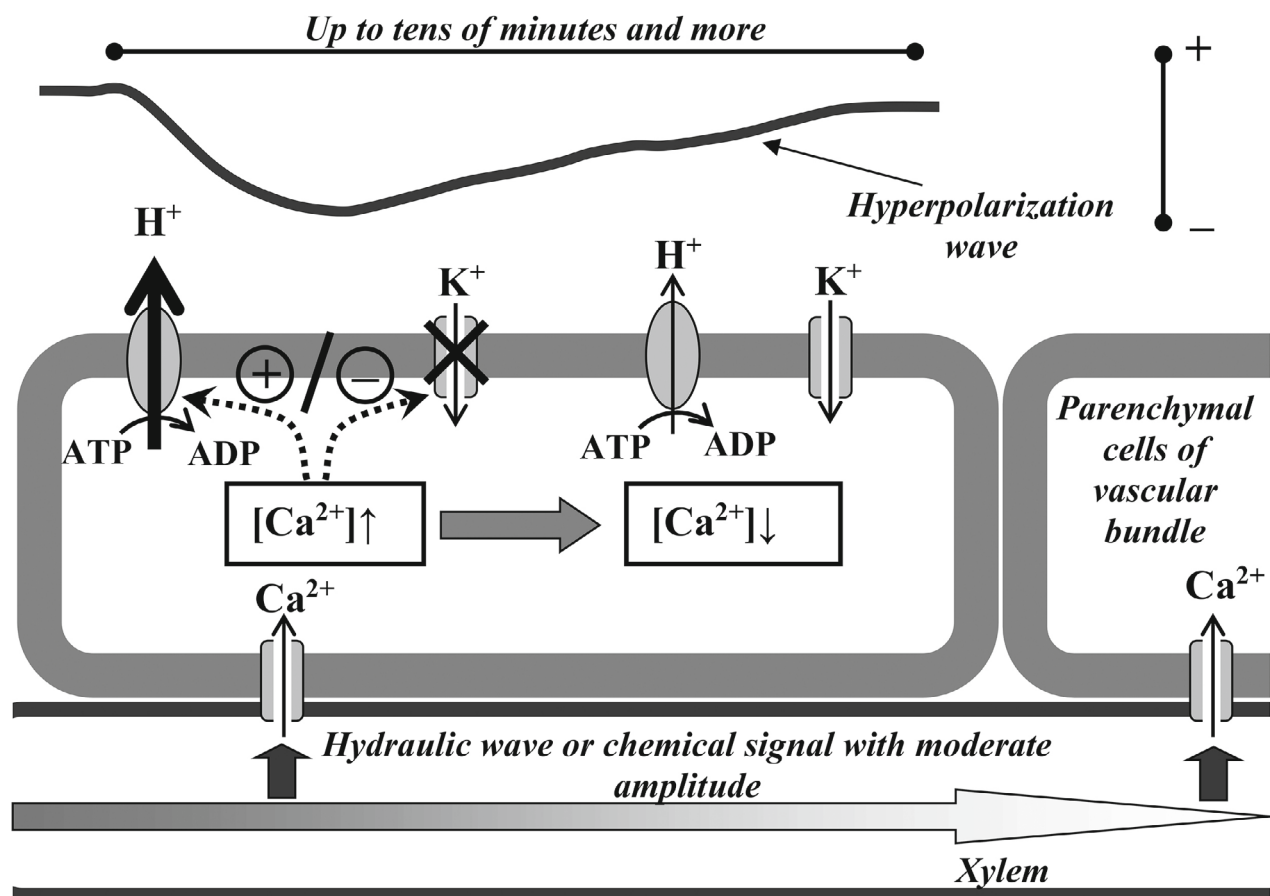
Up to tens of minutes and more

Hyperpolarization wave

H^+

K^+

H^+

K^+

ATP ADP

$+$/$-$

$[Ca^{2+}]\uparrow$

$[Ca^{2+}]\downarrow$

ATP ADP

Parenchymal cells of vascular bundle

Ca^{2+}

Ca^{2+}

Hydraulic wave or chemical signal with moderate amplitude

Xylem

Fig. 3. System potential in higher plants and schematic presentation of potential mechanism of its generation and propagation along the vascular bundles in plants. Possible effects of a moderate increase of Ca^{2+} concentration in cytoplasm on H^+-ATPase (activation) and on inwardly-rectifying K^+-channels of plasma membrane (inactivation) are shown by dashed lines.

of SP during local exposure to the H^+-ATPase inducer (fusicoccin); however, nature of the signal causing such activation is still undetermined. We have suggested previously [69-71] that transmission of SP is associated with propagation of the small-amplitude hydraulic signal, which activates mechanosensitive Ca^{2+}-channels in the plasma membrane and causes moderate increase of calcium ion concentration in cytoplasm. There are data available [72, 73] demonstrating that moderate increase of Ca^{2+} concentration could cause activation of the plasma membrane H^+-ATPase, which, in turn, results in hyperpolarization. On the other hand, a number of studies show that the moderate increase of Ca^{2+} concentration in cytoplasm (200-400 nM) causes inactivation of the inwardly-rectifying K^+-channel in the plasma membrane [74, 75], which mediates influx of potassium ions from the extracellular space into the cell cytoplasm. Considering that the inwardly-rectifying K^+-channels and H^+-ATPase of plasma membrane are the main systems of electrogenic ion transport under rest condition [47, 76, 77] (in accordance with the previously conducted theoretical analysis of the developed mathematical model of electrogenesis in the cell of higher plants [47]),

decrease of permeability of K^+-channels should result in hyperpolarization. In the process, development of hyperpolarization would be due to decrease of the contribution of electrical conductance of the inwardly-rectifying K^+-channels to the total conductance of the plasma membrane. The latter could be confirmed by the changes of membrane potential (E_M) described in a simplified manner by the equation (1):

$$E_M = \frac{E_P + g_K/g_P \, E_K}{1 + g_K/g_P}, \tag{1}$$

where E_P — electromotive force (EMF) of H^+-ATPase (around -450 mV) and E_K — Nernst potential for potassium ions (around -100 mV; based on [49, 76, 77]) under conditions of reduction of conductance of K^+-channels (g_K) with respect to conductance of H^+-ATPase (g_P). The presented equation based on the parallel electrical circuit of the inwardly-rectifying K^+-channels and H^+-ATPase provides stationary solution for the membrane potential.

Hypothesis on inactivation of the inwardly-rectifying K^+-channels is in good agreement with the suppression of generation of SP by the action of the

specific blocker of the K$^+$-channels, tetraethyl ammonium [65]. The main advantage of the suggested hypothesis is its ability to explain association between VP and SP, because the decrease of amplitude of the hydraulic wave (with the decrease of the stimulus strength during drought development or with the increase of the distance from the zone of stimulation [51, 53, 68-71]) should decrease influx of Ca^{2+} into the cell, which could result in the change of the type of ES: long-term wave of depolarization (in the case of large or moderate increase of calcium ion concentration in cytoplasm) is replaced with the hyperpolarization wave (in the case of slight increase of Ca^{2+} concentration). However, it should be mentioned that the suggested mechanism is potentially compatible with the chemical hypothesis of the signal transmission; in this case induction of the calcium ion influx could occur through the ligand-dependent Ca^{2+}-channels [48].

Hence, common feature of AP, VP, and SP generation involves changes in activity of the H$^+$-ATPase in plasma membrane, which is in good agreement with the key role of the P-type ATPases in maintenance of a number of physiological processes in plants and in responses to the action of environmental factors [78, 79], including changes in activity of H$^+$-ATPase under the action of abiotic and biotic stressors. The key mechanism of the changes of H$^+$-ATPase activity is phosphorylation of amino acid residues of the R-domain at the C-end of the enzyme [78, 79]: phosphorylation of Thr947 facilitates attachment of the 14-3-3 proteins to the C-end and causes activation of the enzyme; and, on the contrary, phosphorylation of a number of other amino acid residues disrupts binding of the 14-3-3 proteins and results in inactivation of H$^+$-ATPase. It must be mentioned that the Ca^{2+}-dependent inactivation of H$^+$-ATPase, which could be prevented by the treatment with the H-7 protein kinase inhibitor [46] is likely associated with phosphorylation of one of the amino acid residues (Ser944, Thr942, Tyr946) and disruption of binding of the 14-3-3 proteins to the C-end of the enzyme [79].

It is likely that the direct contributions of the H$^+$-ATPase to formation of electrical signals vary. In particular, in the case of AP, elimination of the H$^+$-ATPase inactivation affects only slightly the shape and amplitude of the signal, but completely suppresses the accompanying alkalization of apoplast [46, 47]. On the other hand, inactivation of H$^+$-ATPase is the main mechanism of VP generation [48], because decrease of activity of this transporter results in significant suppression of the long-term depolarization wave, which is the basis of variation potential [49, 64, 80].

More complicated pattern is observed in the case of SP. The main hypothesis [66, 67, 69-71] describing mechanisms of SP suggests increase of the absolute activity of H$^+$-ATPase; however, this suggestion contra-

dicts the data on alkalization of apoplast during development of the system potential [66]. Similar alkalization observed during inactivation of H$^+$-ATPase in the course of generation of AP [46, 47] and VP [25, 27] more likely indicates decrease of activity of this transporter. The suggestion on increase of the relative activity of H$^+$-ATPase due to Ca^{2+}-dependent decrease of the activity of inwardly-rectifying K$^+$-channels [74, 75] is more in line with such data, because development of hyperpolarization should decrease active transport of protons from the cell and results in alkalization of apoplast due to increase of the proton electrochemical gradient directed against such transport.

In conclusion to this section, it must mention specifically that the changes of pH that accompany the changes of activity of the plasma membrane H$^+$-ATPase during development of ES are to a large degree associated with the existence of the oppositely directed proton flows. In accordance with the mathematical model of electrogenesis in the cells of higher plants previously developed in our work [47, 77], such flows may be due to activities of H$^+$/K$^+$-antiporters and 2H$^+$/Cl$^-$-symporters, and leakage of protons through the plasma membrane. In particular, such flows could facilitate rapid transport of protons inside the cell during decrease of compensating efflux of H$^+$ under conditions of H$^+$-ATPase inactivation. Potentially the abovementioned oppositely directed proton flows could be regulated by certain factors. However, such regulation is not required for realistic description of electrical responses in plants during modeling [47, 76, 77], that is why the hypothesis on regulation of the inward H$^+$ flows is, most likely, excessive in the case of the cells of higher plants.

In general, participation of the changes of H$^+$-ATPase activity in generation of all main types of ESs allows suggesting that such changes could play a certain physiological role; in particular, the idea of involvement of such changes in regulation of photosynthetic processes by electrical signals in higher plants attracts attention of researchers [23].

CHANGES OF PLASMA MEMBRANE H$^+$-ATPase ACTIVITY AS A MECHANISM UNDERLYING EFFECTS OF ELECTRICAL SIGNALS ON PHOTOSYNTHESIS

As was mentioned above, there are several arguments showing similarities in the decrease of absolute activity of the plasma membrane H$^+$-ATPase during generation of all three types of ESs; first of all, this is illustrated by the fact of alkalization of apoplast observed during generation of AP [46, 47], VP [25, 27], and SP [66]. If such decrease indeed causes the ES-induced inactivation of photosynthesis, it can be expected that this inactivation would be observed during propagation of

all three types of ES. According to the literature data, AP [14, 81, 82], VP [16, 24-30, 83], and SP [66, 71] could cause similar changes in the intensity of photosynthetic processes including decrease of intensity of CO_2 assimilation, decrease of the quantum yield of the photosystem II, and increase of non-photochemical quenching of the chlorophyll fluorescence.

The ES-induced responses of photosynthesis include short-term (5-10 min) and long-term (tens of minutes, and, probably hours) inactivation [6, 7, 23]. In some cases, only long-term inactivation could be observed in plants (see, for example, papers published by Hlaváčková et al. [10], Herde et al. [84], and Sherstneva et al. [85]). It was shown in a number of studies [14, 26, 35] that the decrease of CO_2 concentration in the medium results in inactivation of the light-dependent reactions of photosynthesis similar to the one caused by ES and reduces the amplitude of photosynthetic responses induced by electrical signals; however, no complete suppression of the short-term and long-term changes of the parameters of the light-dependent reactions has been observed. It has been suggested based on this information [6, 23] that the short-term, and, probably, long-term inactivation of photosynthesis are associated with two different types of mechanisms:

(i) With the decrease of intensity of the dark reactions of photosynthesis resulting in the decrease of the ADP/ATP and $NADP^+$/NADPH ratios in the chloroplast stroma and, respectively, in suppression of the processes of the light-dependent reactions due to increase of the electrochemical gradient on the thylakoid membrane (results of reduction of H^+-ATP-synthase activity due to substrate deficit) and disruption of the electron leakage from the electron-transport chain [14, 26]. Decrease of the leaf mesophyll conductance to CO_2 [24] and, probably, closing of stomata [21] are the suggested mechanisms of suppression of the dark reactions of photosynthesis.

(ii) With the suppression of the light reactions of photosynthesis that is not caused by the inhibition of Calvin cycle, which, potentially, also could have different mechanisms (in particular, increase of non-photochemical quenching [27, 29] and decrease of activity of the ferredoxin-$NADP^+$-reductase [26]).

There are several hypotheses explaining mechanisms of photosynthesis inactivation [23]. Among them suppression of activity of the Calvin cycle enzymes due to influx of Ca^{2+} in the cytoplasm and further to chloroplast stroma [81] and inactivating effects of ROS (likely H_2O_2) [83] should be mentioned. In the case of long-term inactivation of photosynthesis involvement of the stress hormones (abscisic and jasmonic acids [10, 11, 50]), which trigger stomata closing and suppression of photosynthesis, has also been considered. At the same time, reversible inactivation of plasma membrane H^+-ATPase seems to be the most plausible mechanism

of the development of the ES-induced photosynthetic responses in plants [6, 23]. It must be mentioned, first of all, that such inactivation could be the consequence of all the mentioned mechanisms. In particular, it is known that the increase of calcium ion concentration could result in suppression of the plasma membrane H^+-ATPase [86], spread of H_2O_2 is considered to be associated with activation of Ca^{2+}-channels, influx of calcium ions, and inactivation of H^+-ATPase [6, 54-56]. The effect of abscisic acid on photosynthesis also could be mediated by the decrease of activity of H^+-ATPase [87, 88].

The results of our earlier studies [88, 89] demonstrate that the moderate increase or decrease of the initial activity of H^+-ATPase in the plants treated with activators (fusicoccin) or inhibitors (sodium orthovanadate) of this ion transporter results, respectively, in the increase or decrease of the photosynthetic response developing during the further induction of VP. These results confirm participation of H^+-ATPase in formation of the ES-induced changes in photosynthesis, because while the value of relative change of its activity remains constant, the absolute value of such change increases in the case of prior activation of H^+-ATPase or decreases in the case of its prior inactivation, which would result in the increase or decrease of the ES-induced photosynthetic response, respectively.

Changes of intracellular and extracellular pH that accompany inactivation of the H^+-ATPase are considered as a possible mechanism of development of the ES-induced photosynthetic responses [2, 6, 23]. Several arguments exist supporting this hypothesis. Firstly, it was shown in a considerable number of studies that generation of different types of ES in plants is accompanied with the increase of pH in apoplast, and decrease of pH in cytoplasm [25, 27, 45, 46, 66, 85]. Moreover, it was revealed by indirect methods that acidification of the chloroplast stroma and lumen accompany generation of VP [90]. Furthermore, it was shown in some studies [91, 92] that there is a strong association between the changes of pH and parameters of photosynthesis, which supports their role in induction of photosynthetic responses. Secondly, it was shown that the artificial induction of pH changes by exposure of leaves parts to protonophores [27] or by inhibiting H^+-ATPase activity in protoplasts with sodium orthovanadate [89] results in induction of photosynthetic responses, which are similar to the ones observed during propagation of ES (decrease of quantum yield of photosystem II and increase of non-photochemical quenching). Thirdly, acidification of the chloroplast incubation medium that mimics decrease of pH in cytoplasm during ES development also induces photosynthetic responses similar to the responses caused by electrical signals [25, 27, 85]; amplitude of such responses linearly correlate with the degree of pH changes [27, 85]. Similar effect was revealed during

perfusion of the cells of Charophyte algae with acidified solutions [93].

It was shown in our previous studies [91, 92] that the increase of extracellular pH accompanying VP is associated primarily with the decrease of photosynthetic assimilation of CO_2, while the decrease of intracellular pH is associated with the increase of non-photochemical fluorescence quenching. Based on these facts it could be suggested [6, 23] that the ES-induced alkalization of apoplast mainly affects supply of CO_2 to the cells, while acidification of the cytoplasm, stroma, and lumen of chloroplasts could directly affect reactions of the light-dependent stage of photosynthesis. This suggestion is in good agreement with the ES-induced decrease of conductance of the leaf mesophyll to CO_2 [24] and with the observed changes of the light-dependent reactions of photosynthesis induced by electrical signals, which are not associated with inactivation of the dark reactions [26, 27, 29].

The pH-dependent decrease of the CO_2/HCO_3^- ratio could be suggested as a simple mechanism of the effect of alkalization of apoplast on the supply of CO_2 into photosynthesizing cells [23], because the charged form penetrates biological membrane much less than the neutral one [94]. This suggestion was pre-confirmed by the analysis of the simplified mathematical model describing effects of inactivation of H$^+$-ATPase on the fraction of the neutral form of CO_2 [95]; however, further investigation of the more detailed photosynthetic model of a leaf did not confirm significant contribution of this mechanism to the decrease of activity of photosynthesis during alkalization of apoplast (at least for the stationary CO_2 flow described for an uniform apoplast and used parameters of the model) [96, 97].

The alternative hypothesis describing the ES-induced effect of pH changes on the leaf mesophyll conductance to CO_2 was suggested by Gallé et al. [24]. In accordance with this theory such changes affect conductance of aquaporins, which play an important role in supplying carbon dioxide to the cells of higher plants [98] and could be controlled by pH [99-101]. Such hypothesis is in good agreement with the results of modeling [97] demonstrating dependence of the stationary intensity of photosynthesis on the conductance of plasma membrane to CO_2; however, the literature data [99-101] show that the conductance of aquaporins decreases with acidification of cytoplasm, but not with alkalization of apoplast. Despite the fact that both processes accompany generation of ES [25, 27], our data indicate [91, 92] very weak association of the cytoplasm acidification with the decrease of intensity of the dark reactions of photosynthesis; in other words, there is certain contradiction between the hypothesis on participation of aquaporins in the development of ES-induced photosynthetic responses and experimental peculiarities of these responses.

Hence, the problem of specific mechanisms of the effect of pH changes on the supply of CO_2 to mesophyll cells remains unsolved. Potentially the revealed contradictions could be explained by uneven spatial distribution of carbonic anhydrases, which accelerate significantly mutual conversion between CO_2 and HCO_3^-, because such heterogeneity could provide local pH-dependent changes of the ratio between the neutral and charged forms of carbon dioxide, which would affect its penetration through the plasma membrane without significant changes of the average concentration of these forms in apoplast (in the suggested photosynthetic model of a leaf [96, 97] such possibility was not considered). Some studies demonstrating that carbonic anhydrases and aquaporins function together in the plasma membrane [102] and that carbonic anhydrases affect mesophyll conductance to CO_2 [103] provide support to this hypothesis.

It must be mentioned that the ES-induced closing of stomata, which could be involved in the long-term inactivation of photosynthetic processes [21], is also associated with the suppression of H$^+$-ATPase activity, because the level of response could be modified by changing initial activity of this transporter [36]. At the same, the direct mechanism of the stomata closing is, most likely, not inactivation of H$^+$-ATPase, but rather changes of activity of ion channels facilitated by this inactivation, which results in the efflux of ions from the guard cells. In particular, significant efflux of chloride ions was demonstrated in a number of studies, which accompanied generation of electrical signals of different types [6, 7, 48, 66].

Direct effect of the cytoplasm acidification on the parameters of the light stage of photosynthesis is likely due to the flow of protons from cytoplasm to stroma and chloroplast lumen [23]. The decrease of pH in stroma and lumen during development of VP was indirectly confirmed in our previous study based on the measurements of both the electrochromic shift of the leaf absorption and light scattering at 535 nm [90], which indicate proton transport through chloroplast envelopes and thylakoid membranes.

According to the studies by Alte et al. [104] and Benz et al. [105], decrease of the chloroplast stroma pH could cause increase of affinity of the ferredoxin-NADP$^+$-reductase to the specific binding sites (Tic62 and TROL), which results in the increase of the distance between the enzyme and photosystem I, thus decreasing electron flow at the acceptor part of this photosystem. This mechanism is in agreement with the VP-induced increase of losses at the acceptor side of the photosystem I [26], which practically is independent on the intensity of the dark reactions of photosynthesis. It is likely that this mechanism could also facilitate the ES-induced activation of the cyclic electron flow around the photosystem I [28], because decrease
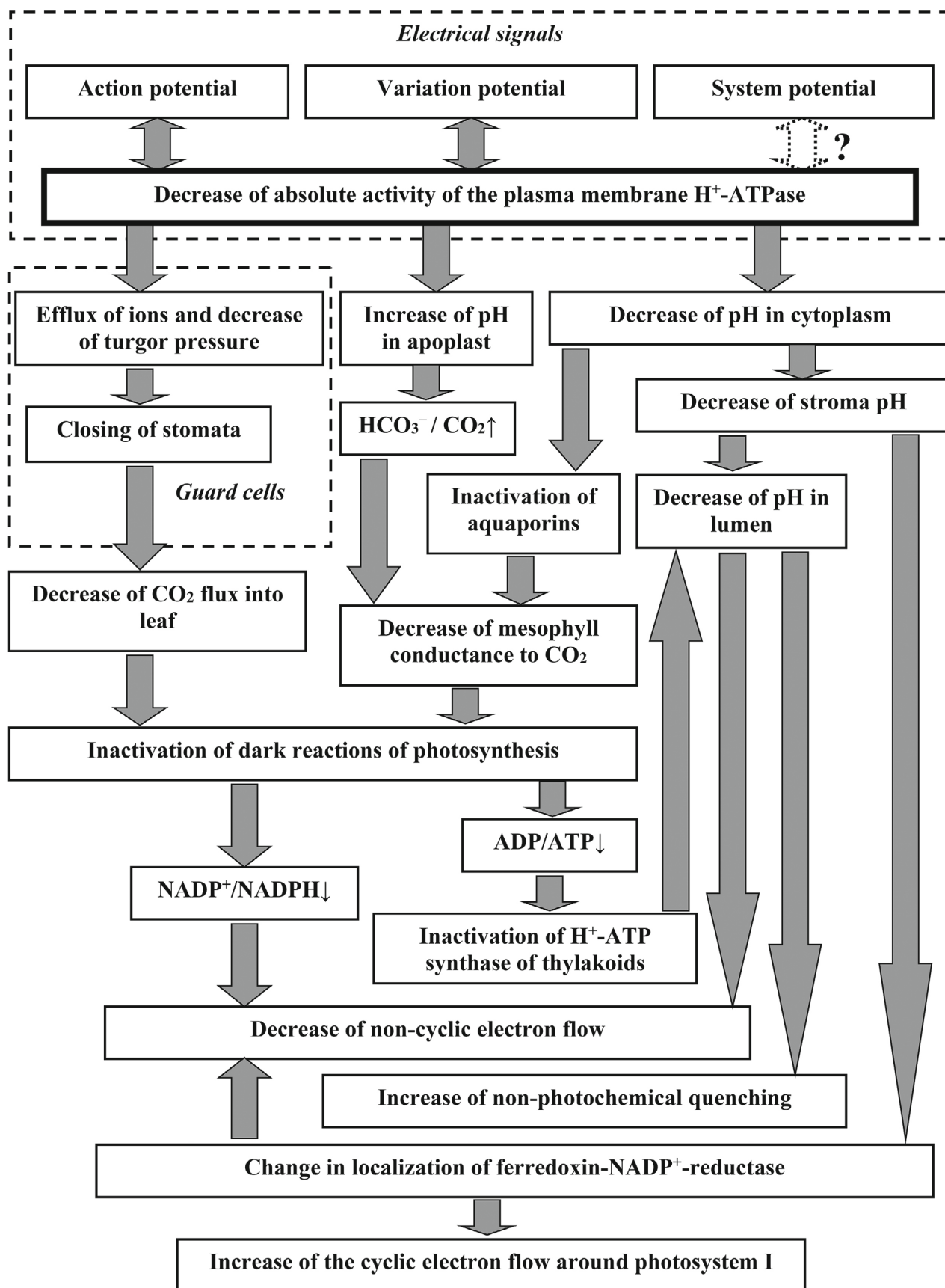
Fig. 4. Schematic presentation of possible pathways involving inactivation of the plasma membrane H^+-ATPase in regulation of photosynthesis by electrical signals. The variant suggesting participation of the inwardly-rectifying K^+-channels in hyperpolarization is presented for SP.

of the non-cyclic flow, which competes for the substrate (reduced ferredoxin) should result in the increase of other flows using the same substrate [106].

The ES-induced acidification of the chloroplast lumen would firstly induce increase of the energy-dependent component of the non-photochemical fluorescence quenching, because electrical signals could cause significant increase of this component [30], for which close association with the lumen pH was demonstrated [107-109]. Direct decrease of the electron flow through the photosynthetic electron-transport chain also could be the result of acidification of the chloroplast lumen, because one of the limiting steps of this process is oxidation of plastoquinones in the cytochrome b_6f complex [110, 111]; it is generally recognized that this step is highly sensitive to the lumen pH and slows down with the increase of proton concentration. Potentially, the component of non-photochemical fluorescence quenching occurring due to the shift of the main pigment−protein light-harvesting complex (state transition) could be another 'target' of the pH decrease in the chloroplast lumen [112], as it has been shown [29] that in the absence of illumination and, correspondingly, change of the activity of the dark reactions of photosynthesis, ES could cause changes in the distribution of the absorbed light between the photosystems I and II.

Hence, the decrease of the absolute value of the plasma membrane H⁺-ATPase activity, which accompanies generation of AP, VP, and, likely, SP, results in the increase of extracellular and decrease of intracellular pH and, consequently, causes inactivation of photosynthesis via several interrelated mechanisms (Fig. 4).

One of the presumed results of the ES-induced changes of photosynthesis in the intact parts of the plant is increase of tolerance of the photosynthetic apparatus to the action of stressors on these parts [6, 7, 23, 31]. This tolerance increase would be very significant for the plant in the case if the local exposure to the stressor that induces electrical signals, is a precursor of the action of adverse factors on the other parts of the plant organism [6, 7]. The mechanisms of ES-induced increase of the photosynthetic apparatus tolerance could be classified into several groups [6, 7, 23, 31].

(i) Positive effect of ESs on tolerance of the photosystem II in the case of moderate intensity of the stressors (exemplified with the higher and lower temperatures) [34, 39] could be associated with the increase of energy-dependent component of the non-photochemical fluorescence quenching [30] and activation of the cyclic electron flow [28], which represent effective mechanisms of protection of the photosynthetic apparatus under the action of a wide spectrum of stresses [107-100, 113, 114].

(ii) In the case of exposure to high temperature, effect of ESs on the stability of the photosynthetic apparatus has a more complicated nature [35, 36]: the decrease of damage in the photosystem I is accompanied by the enhanced damage of the photosystem II; these processes are interrelated [37]. This result could be explained by the hypothesis [115, 116] suggesting that, under conditions of extreme intensity of the stressor action, damage of the photosystem II that is capable of relatively rapid repair, could lead to preservation of the photosystem I due to the stoppage of electron influx from water, decrease of the excessive reduction of the electron transport chain, and, as a result, decrease of ROS generation. It is worth mentioning that preservation of the photosystem I is also important for the following repair of the photosynthetic apparatus [23], because in this case functioning of the cyclic electron flow and ATP synthesis is preserved.

(iii) Considering that the increase of ATP content in leaves is an important result of the ES-induced photosynthetic responses [16], it can be suggested that this increase comprises the mechanism of acceleration of the photosynthetic apparatus repair after the damaging action of stressors. Positive effect of ATP on the resistance of the photosynthetic apparatus in plants [117] and the data on ES-induced acceleration of the photosystem II repair [34] support this hypothesis.

Result of the ES-induced increase of stability of the photosynthetic apparatus is general increase of the plant resistance, which is manifested in the lesser suppression of growth [36] and electrical activity [40] under conditions of systemic exposure to stressors.

CONCLUSIONS

The presented review demonstrates that formation of all types of electrical signals in higher plants is associated with the changes in activity of the plasma membrane H⁺-ATPase; furthermore, inactivation of H⁺-ATPase plays an important role in generation of action potentials and variation potentials. In the case of system potential, the problem of particular changes of the H⁺-ATPase activity is more complicated: on the one hand, one cannot rule out increase of the absolute activity of the transporter, which could be due to the two-phase dependence of the activity on Ca^{2+} concentration in cytoplasm (activation with small increase of concentration and inactivation with moderate and high increase). On another hand, a number of arguments (alkalization of apoplast during generation of system potential, role of potassium channels in this generation) indicate high probability of participation of the relative increase of the H⁺-ATPase activity in the generation of system potential; this increase is due to the Ca^{2+}-dependent inactivation of the inwardly-rectifying K⁺-channels in plasma membrane with slight increase of the calcium ion concentration. Absolute activity of the H⁺-ATPase could decrease in the process due to increase of the electrochemical

proton gradient directed inward the cell during hyperpolarization. Increase of the electrochemical gradient could also decrease total efficiency of H^+ transport from the cell due to activation of the systems of secondary active transport (such as proton-anion symporter [118]) and enhancement of passive H^+ flows into cytoplasm [119].

It seems likely that the decrease of absolute activity of the plasma membrane H^+-ATPase is the main mechanism of inactivating effect of action potentials, variation potentials, and, probably, system potential on photosynthesis. Inactivation of photosynthesis induced by the electrical signals is manifested by the decrease of CO_2 assimilation, quantum yields of photosystems I and II, and non-cyclic electron flow, and by the increase of non-photochemical fluorescence quenching and cyclic electron flow around the photosystem I. In the process, the induced by electrical signals increase of pH in apoplast facilitates decrease of CO_2 supply to the cell, inactivation of the dark reactions of photosynthesis and, as a result, suppression of the light-dependent reactions of photosynthesis; in turn, decrease of pH in cytoplasm and, as a result, in stroma and chloroplast lumen cause additional suppression of the light-dependent reactions of photosynthesis.

The result of the photosynthetic responses induced by electrical signals is, most likely, increase of tolerance of the photosynthetic apparatus to the action of stressors and enabling its following repair. Such changes, in turn, provide contribution to the general increase of resistance of the plant to the systemic action of adverse factors and facilitate the plant survival under changing environmental conditions.

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