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REVIEW

Ion Channels in Electrical Signaling in Higher Plants

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Abstract—Electrical signals (ESs) appearing in plants under the action of various external factors play an important role in adaptation to changing environmental conditions. Generation of ES in higher plant cells is associated with activation of Ca^{2+}, K^+, and anion fluxes, as well as with changes in the activity of plasma membrane H^+-ATPase. In the present review, molecular nature of the ion channels contributing to ESs transmission in higher plants is analyzed based on comparison of the data from molecular-genetic and electrophysiological studies. Based on such characteristics of ion channels as selectivity, activation mechanism, and intracellular and tissue localization, those ion channels that meet the requirements for potential participation in ES generation were selected from a wide variety of ion channels in higher plants. Analysis of the data of experimental studies performed on mutants with suppressed or enhanced expression of a certain channel gene revealed those channels whose activation contributes to ESs formation. The channels responsible for Ca^{2+} flux during generation of ESs include channels of the GLR family, for K^+ flux – GORK, for anions – MSL. Consideration of the prospects of further studies suggests the need to combine electrophysiological and genetic approaches along with analysis of ion concentrations in intact plants within a single study.

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INTRODUCTION

Plants in nature are subjected to the action of various adverse environmental factors. In order to develop coordinated systemic response to the action of environmental factors long-distance signal transmission is required. Three types of long-distance signals are recognized in plants – chemical, hydraulic, and electrical, which differ both in nature and in the rate of transmission. Electrical signal (ES) with propagation rates up to tens of centimeters per second, together with hydraulic ones, are considered as rapid long-distance signals [1-4].

Propagation of ESs triggers a wide range of functional changes in the non-affected parts of the plant. The ES-induced responses include changes in photosynthesis activity and transpiration, enhancement of respiration, changes in ATP content, expression of protective genes, and others [1, 3, 5]. Such changes play an important role in the plant adaptation to the changing environmental conditions. It is known that the mechanisms of induction of ES-mediated systemic responses in plants are based on the changes of ion concentrations during the generation of ESs with the shifts in Ca^{2+} and H^+ concentrations playing the most important role [5, 6]. Ion flows causing the change in concentration appear as a result of changes in the activities of ion transport systems, primarily ion channels [2, 3, 7]. However, molecular nature of such channels remains poorly understood.

Elucidation of the molecular nature of ion channels participating in generation of ESs in higher plants is challenging. Firstly, it must be mentioned that investigation of the parameters of ESs and mechanisms of their generation was conducted with different plant species. In particular, plants exhibiting locomotion comprise traditional objects in the area of plant electrophysiology. Another model object, for which a significant amount of data on the mechanisms of ES generation was accumulated and involvement of ion channel in these processes

Abbreviations: AP, action potential; ES, electrical signal; SP, system potential; VP, variation potential.

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was for the first time demonstrated, are giant cells of charophyte green algae that are very simple to work with from methodological point of view [8-11]. At the same time, Arabidopsis (*Arabidopsis thaliana*) is the main object of molecular genetics research, but for which only few studies devoted to investigation of ES are available. All the facts mentioned above do not allow direct comparison of the electrophysiological and molecular genetics data in the literature. In this review we attempted to make such comparison: we present available information on the nature of ion channels underlying the mechanisms of ES generation and on the ion channels with identified genetic association, as well as we suggest the most probable participants of the process of ES generation in higher plants based on the analysis of the data.

ELECTRICAL SIGNALS IN HIGHER PLANTS

The values of membrane electric potential in the plant cells at rest are at significantly more negative level in comparison with the animal cells, which is below −100 mV, and for some plants and plant tissues even below −200 mV. Such high values are due to the significant contribution of the metabolic component to the total value of electric potential, which is created due to the functioning of the plasmalemma H^+-ATPase [6, 8]. Electric transmembrane potential, as a component of electrochemical gradient, is a moving force of membrane transport, including ion flows occurring during generation of ESs. At present, three different types of ESs are recognized in plants: action potential (AP), variation potential (VP), and system potential (SP) [1, 3, 7, 12]. The latter is not considered in this review due to insufficient knowledge on the mechanisms of its generation. Classification of the signals into different types is based on several characteristics including direction of the potential change (de-/hyperpolarization), duration of electrical reaction, nature of its propagation, as well as typical stressors triggering the signal of a certain type.

Action potential (AP) comprises a transient depolarization with amplitude of several tens of mV that has typical pulse shape appearing after the threshold is reached according to the "all-or-none" principle [1, 6, 12, 13]. The mentioned properties of plant AP are similar to those of classic nerve pulse. The main differences are associated with the time-characteristics of the reaction: duration of AP in plants is thousand-fold longer than the duration of nerve pulse – from several seconds in plants with locomotion such as mimosa and Venus flytrap, to several tens of seconds in regular plants without locomotion [1, 13].

The mechanism of AP generation in plant cells (Fig. 1) also differs from the classic Na^+/K^+-scheme of the nerve pulse. Formation of depolarization phase in plants is associated with influx of Ca^{2+} and efflux of anions, primarily Cl^-, as well as, likely, with the temporary decrease of the H^+-ATPase activity. In the process, Ca^{2+} ions play predominantly signaling role inducing anion flow and inactivation of the H^+-ATPase [1, 12, 13]. At the same time, the defining role of Ca^{2+} in the change of the level of electric potential during formation of depolarization phase was demonstrated for some plant species [14, 15], which indicates diversity of the mechanism of AP generation in different plant species. Formation of the repolarization phase is associated with the efflux of K^+ mediated by depolarization and with reactivation of H^+-ATPase due to removal of the excess of Ca^{2+} ions [3, 8, 13].

Propagation of AP within the plant (Fig. 1) occurs without significant decrease of amplitude and rate, which usually is from the fraction of a centimeter to several centimeters per second, reaching 8-10 cm/s in the plants exhibiting locomotion [1, 7, 16]. The decrement-free propagation of AP indicates that this process is active: generation of AP induces depolarization in the neighboring cells up to threshold levels due to appearance of local currents followed by generation of AP at these sites [8, 12, 13]. In general, in can be stated that there are fundamental similarities between the mechanisms of propagation of a nerve pulse and propagation of AP in plants, despite the lower rate of the latter (by 2-3 orders of magnitude). However, the issue of the main pathways of AP transmission in higher plants remains unresolved. Conducting bundles in higher plants are generally recognized as a pathway of systemic transmission of all types of the signals, including electrical [1, 5, 7]. It has been assumed that the phloem cells both sieve elements and phloem parenchyma are responsible for undamped transmission of AP [1, 3]. There is also radial propagation of AP from the conducting bundles to the neighboring cells through plasmodesma connections, probably as a fading signal [1, 12, 13].

Various non-damaging stimuli such as changing of temperature, illumination intensity, touching, and others cause generation of AP. The mechanisms of transformation of the energy of stimulus into changes of potential and role of certain ion channels in this process are considered in the respective reviews [3, 7, 17]. It must be emphasized that generation of AP in plants, similar to the nerve fibers, could be also induced by the direct electrical stimulation [15], which indicates certain role of voltage-gated ion channels in the induction of AP.

Variation potential (VP) (Fig. 1), similar to AP, comprises a transient depolarization with amplitude of several tens of mV, but it has much longer duration, up to several minutes, and irregular shape [1, 3, 7, 13, 16]. While considering long duration of VP, which often results in its description as a slow wave potential (SWP), it must be emphasized that the reason for it is slow phase of repolarization in VP with duration of depolarization phase usually not exceeding several seconds as in the case of AP.

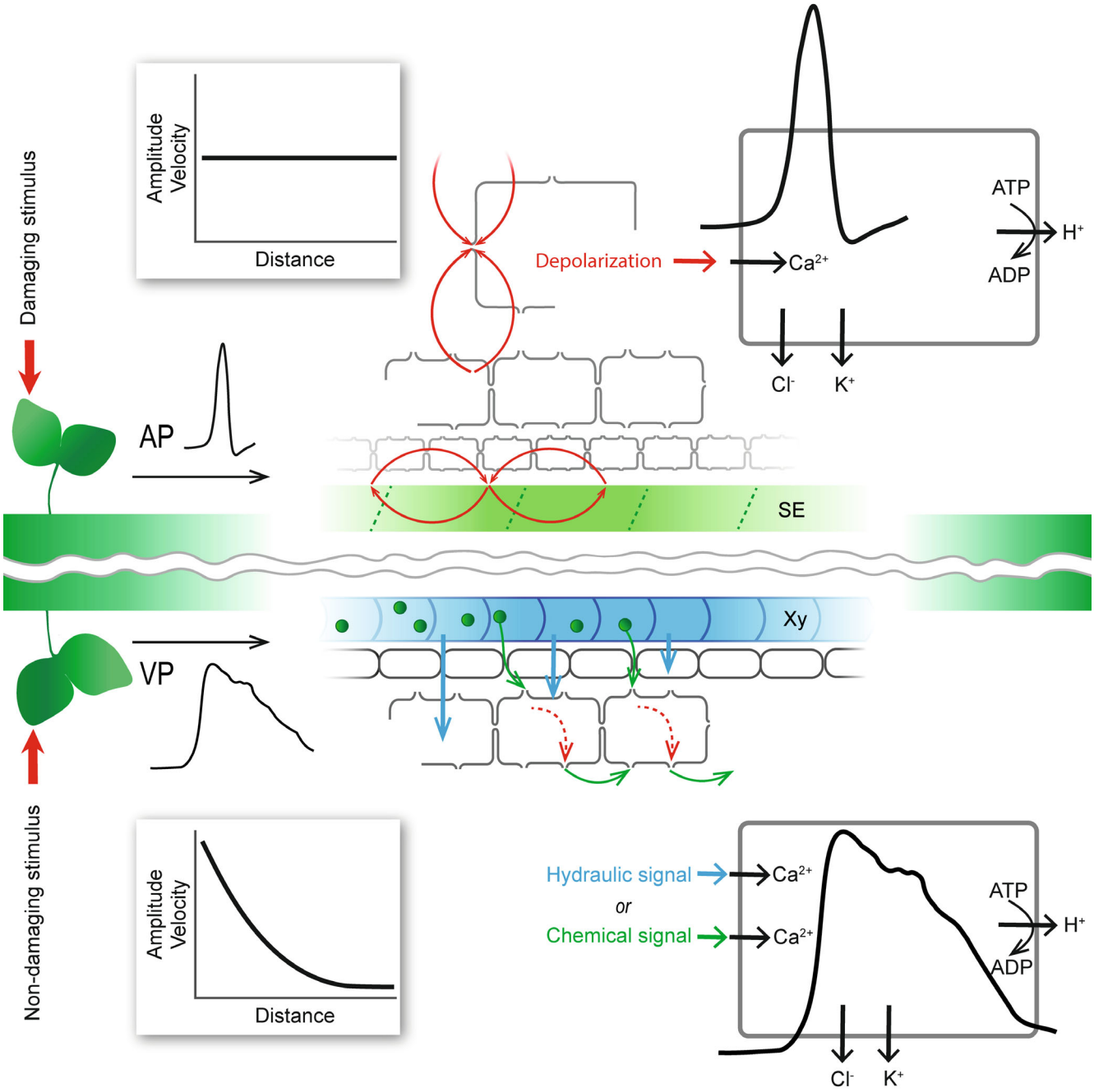

Fig. 1. Scheme for generation and propagation of action potential (AP) and variation potential (VP) along the conductive plant tissues. Non-damaging stimulus, which is transmitted primarily along the phloem (sieve elements, SE) due to emergence of local currents (marked with red arrows). Damaging stimulus induces VP, which is propagated via transmission along xylem (Xy) of the chemical (marked with green dots) or hydraulic (marked with blue arrow) signals. Mechanisms of AP and VP generation are presented in the scheme on the right (see explanations in the text).

VP, unlike AP, does not function according to the "all-or-none" rule, its amplitude and duration depend on the type of stimulus [18, 19] and surface area of damage [16]. Rate of propagation of VP is 0.1-10 mm/s. With the increasing distance form the damage site decrease of the amplitude and rate of signal propagation are observed [1, 3, 6, 13]. Generation of VP is induced by the damaging stimuli [1, 3], such as burn [18, 19], mechanical damage [18, 20, 21], and heating [18, 19, 22].

Transient suppression of the plasmalemma H^+-ATPase activity has been considered for a long time as the only mechanism of VP formation (Fig. 1) [13, 16]. Later it was shown that the passive flows of Ca^{2+}, Cl^-, and K^+ ions that appear, likely, during activation of corresponding ion channels also contribute to generation of VP together with the transient inactivation of the proton pump [7, 23, 24]. Similar to the case of AP, in the initial step of VP generation there is influx of Ca^{2+} into the cell,

which causes decrease of the H^+-ATPase activity that lasts much longer than in the case of AP. Flow of anions, such as Cl^-, also contributes to formation of depolarization phase [5, 12, 25, 26]. Formation of repolarization phase occurs due to restoration of the H^+-ATPase activity, as well, likely, due to efflux of K^+ from the cell [1, 26]. Despite the fact that both AP and VP involve transport of the same set of ions (Ca^{2+}, Cl^-, K^+, H^+), ion transport systems responsible for their movements are, likely, different in both types of ESs. This is indirectly confirmed by the fact that VP could appear in the period of absolute refractory of AP [8, 16].

Unlike AP, VP is not a self-propagating ES (Fig. 1), but comprises a local electrical reaction induced by the hydraulic or chemical signal [1, 5, 7, 26]. The possibility of VP induction by artificially increasing pressure [27] supports the role of hydraulic wave in its induction, which suggests activation of mechanosensitive ion channels [1, 16, 26]. Propagation of the chemical signal from the zone of damage is assumed to be realized through the diffusion of the 'wound substance' along the conducting bundles, which induces influx of Ca^{2+} into the cell. According to the modern notion, reactive oxygen species (ROS) produced by NADPH-oxidases, probably respiratory burst oxidase homolog D (RBOHD), could function as such signaling molecules [28]. Systemic spread of H_2O_2 has been demonstrated during the action of the typical VP-inducing stimuli – during mechanical damage, heating, and excessive illumination [28-30]. In turn, Ca^{2+} is capable of activating RBOHD causing increase of H_2O_2 production [7, 31], which, consequently, could facilitate self-sustaining propagation of the signal.

The abovementioned information on the mechanisms of generation and propagation of ESs in higher plants was obtained with the use of a complex of electrophysiological methods including analysis of gradients of electrochemical potentials for different ions, recording the shifts of ion concentrations during excitation, varying ion composition of the medium, inhibitory analysis using ion channel blockers, and others.

It should be mentioned, first of all, that passive flows of ions along the concentration gradient form the basis for generation of ESs [6, 32]. There is a significant electrochemical gradient of Ca^{2+} ions due to low Ca^{2+} concentrations in cytosol and high concentrations in apoplast and intracellular compartments such as vacuole and ER [33]. Content of anions in cytosol is higher than their content in apoplast [34], which together with the negative intracellular electric potential creates a significant outward-directed gradient [6]. For K^+ concentration, which is close to equilibrium at rest, the outward gradient appears during depolarization [6, 32, 35].

Contribution of certain ions to generation of ES initially was investigated by varying ion composition of the medium and evaluation of its effect in the parameters of ESs. Using this approach participation of Ca^{2+}, Cl^-, and K^+ in generation of AP in higher plants was revealed [8, 13]. This approach was also used to establish the source of the Ca^{2+} ion concentration increases in cytosol, which is extracellular depot, because chelating of Ca^{2+} in the extracellular space results in practically complete suppression of AP, but not in the complete suppression of VP [14, 25, 26].

Due to the long duration, generation of even a single ES in plants, unlike in animals, causes noticeable changes of ion concentrations. Relative changes are pronounced more in those compartments, where ion concentration at rest is low – Ca^{2+} on cytosol, K^+ and Cl^- in apoplast [36, 37]. Changes of ion concentrations were recorded with the help of a number of methods such as ion-selective electrodes [24, 38], microelectrode ion flux measurements (MIFE) [39], method of flame photometry and radioactive indicators [8], as well as ion-sensitive chemical or genetically encoded fluorescent sensors [40]. The results indicate influx of Ca^{2+} and efflux of K^+ and Cl^- from the cell during generation of both AP and VP [24, 26, 38]. All aforementioned facts together with the data on the direction of the moving force confirm that the flows of the indicated ions are passive moving through the ion channels along the electrochemical potential gradient.

Classic method for evaluation of activation of ion channels involves measuring of electric resistance of a membrane upon excitation. Generation of AP in plants, similar to the case of nerve pulse, is accompanied by the decrease of membrane resistance, which serves as a proof of activation of ion channels [26]. With regard to VP, it has been believed for a long time that there is no drop in resistance in this case, which served as a main argument suggesting a key role of the electrogenic H^+ pump rather than ion channels in formation of VP [13, 16, 26]. However, later drop in resistance during formation of VP has been demonstrated, which indicated activation of ion channels [25, 26].

The types of ion channels activation of which mediated the revealed ion fluxes forming ES were investigated with the help of blockers. In particular, participation of Ca^{2+}-channels in generation of ES was demonstrated by suppression of ES by the blocker of all types of Ca^{2+}-channels for both the cases of AP [15, 41] and VP [22, 25]. Use of more specific blockers, verapamil, in particular, which blocks voltage-gated channels, as well as neomycin and ruthenium red that block Ca^{2+} efflux from intracellular sources showed participation of corresponding Ca^{2+}-channels in generation of AP [15, 42, 43]. Gd^{3+}, inhibitor of mechanosensitive Ca^{2+}-channels suppressed propagation of VP into unstressed tissues, but not suppressed generation of VP in the zone of stimulation [24]. The blockers of anion channels, such as etacrynic acid, NPPB (5-nitro-2-(3-phenylpropylamino)-benzoic acid), and A-9-C (anthracene-9-carboxylic acid) decrease amplitude and rate of depolarization

in AP [15, 41, 43] and VP [24, 25, 38]. The blocker of K^+-channels, tetraethyl ammonium (TEA), slows down the phase of depolarization in AP, as well as increases amplitude of the pulse and decreases duration of depolarization [15, 41, 43]. The latter indicates that the efflux of K^+ begins at the phase of depolarization in AP, i.e., there is overlapping of depolarizing and repolarizing ion flows. With regards to VP, increase of duration of the depolarization phase under the effect of TEA was demonstrated [24, 25, 38].

Hence, based on the results of electrophysiological analysis it can be concluded that the generation of AP is associated with activation of voltage-gated Ca^{2+}-channels, while generation of VP is associated with activation of ligand-dependent and Ca^{2+}-channels. Anion and K^+-channels participate in the process of generation of both AP and VP. H^+-ATPase of plasmalemma also provides significant contribution to generation of ESs.

The plasmalemma channels have been considered first during analysis of the role of ion channels in generation of ES in higher plants. At the same time, changes of ion concentrations could be due to activation of the channels localized on the membranes of intracellular compartments, such as, primarily, the largest one – vacuole [33]. Electroexcitation of tonoplast and the role of vacuole as a source of Ca^{2+} and Cl^- in generation of ES was observed in charophyte algae [10, 44]. Some studies indicate a similar role of vacuole in other plants [10, 15], in particular, electroexcitation of tonoplast and efflux Ca^{2+} from the vacuole was demonstrate in the Arabidopsis plants [44]. This speaks of the need to consider ion channels of tonoplast during analysis despite the absence of unambiguous data on their role in generation of ESs in higher plants.

It must be mentioned that currently the exact set of ion channels has not been identified for any types of ES, functioning of which is associated with formation of depolarization and repolarization phases of ESs. Based on the analysis of the data of electrophysiological studies, selection of the channels potentially involved in generation of ES should be based on the following criteria: (i) selectivity, the channels mediating Ca^{2+}, K^+, and Cl^- transport are the most interesting; (ii) activation mechanism, possibility of activation during depolarization, mechanical or chemical stimulation; (iii) localization, predominantly on plasmalemma (probably tonoplast) of the cells of conducting tissues.

ION CHANNELS OF HIGHER PLANTS

Currently different groups of ion channels in plants have been characterized with the help of electrophysiological methods, however, as has been mentioned in the review by Demidchik et al. [45], majority of the genes that encode these channels are still unknown. During the last two decades combined analysis of molecular genetics and electrophysiological data have been performed mainly for some groups of ion channels such a K^+-channels [46, 47]. At the same time, the genes encoding Ca^{2+}-channels, in particular plasmalemma Ca^{2+}-channels, have not yet been revealed [45]. In this section the data on the known groups of ion channels that potentially could participate in formation of ESs in plants are summarized (table).

Calcium permeable channels. Despite the widely recognized importance of calcium for plant metabolism, including their role as a secondary messenger, plants do not have canonic ion channels with Ca^{2+}-selective filters. Instead, plants have Ca^{2+}-permeable cation channels that are capable of transporting also other two- and monovalent cations [45, 55], however, for convenience sake this detail is omitted in the majority of publications, and we follow the suite in this review. Based on their electrophysiological characteristics Ca^{2+}-channels are classified into three groups: depolarization-activated Ca^{2+} channels (DACC), hyperpolarization-activated Ca^{2+} channels (HACC), and voltage-independent Ca^{2+} channels (VICC); sometimes mechanosensitive Ca^{2+} channels (MSCC) are distinguished as a subgroup in the last group. It is worth to mention one more time that the genes encoding DACC of plasmalemma have not been identified yet. Ca^{2+}-channels are also classified according to kinetics of their activation: fast channels (responding within milliseconds), slow channels (responding within seconds), and channels with pulsing conductance (response time 1-3 milliseconds) [45, 55].

Using molecular genetics approaches the following families of Ca^{2+}-channels have been identified so far: ionotropic glutamate-like receptors (GLR), cyclic nucleotide-gated channels CNGC), annexins (ANN), two-pore channels (TPCs), Mid1-complementing activity channels (MCA), hyperosmolality-induced $[Ca^{2+}]_i$ increase 1 channel (OSCA1), and piezo channels (Piezo) [45, 55], as well as recently discovered rapidly activated calcium mechanosensitive channel (RMA) [95].

GLRs are integral membrane proteins localized predominantly on plasmalemma and exhibiting activity of a non-selective ion channel, which is belongs to VICC based on electrophysiological properties. Various amino acids and their derivatives could serve as ligands of these receptors, and some activators are specific for individual channels of this family [45, 48, 55]. Expression of the *GLR* genes is observed in the entire plant with certain level of organ- and tissue-specificity (Table 1). Number of GLR are predominantly localized in conducting tissues that mediate propagation of ES [48, 55, 116]. The stimuli inducing activation of GLR are rather diverse and include drought, cold, biotic stresses, and mechanical damages [48, 51, 55, 116]. It is well known that this set of stimuli also induces both changes of membrane potential and intracellular Ca^{2+} concentration [3], which,

Ca^{2+}-, K^+-, and anion channels of higher plants and their characteristics

Channel	Selectivity	Cell localization	Tissue localization	Stimulus	Regulation	References
GLR1.1			leaf, root, ~~flower~~, ~~pods~~	$\downarrow\Psi_w$		[48]
GLR1.2	Ca^{2+}	PM	leaf, root, pollen	cold	Ser, ~~Glu~~	[45, 48-51]
GLR1.3		PM	leaf, stem, root	cold		[48, 49]
GLR1.4	Na^+, K^+, NH_4^+, ~~Cl^-~~	PM	leaf, root, stem		Trp, Met, Phe, Leu, Tyr, Asn, Thr, ~~Glu~~, ~~Gly~~, ~~Arg~~	[45, 48, 52]
GLR2.1			leaf, stem, root, ~~flower~~, ~~pods~~		Glu	[48]
GLR3.1	Ca^{2+}	PM	leaf, root, GC, stem	$\downarrow\Psi_w$, MD	Met	[20, 48, 51, 53]
GLR3.2			leaf, stem, root, CT	NaCl, MD	Ser, Met, Gly	[20, 48, 53]
GLR3.3	$Ca^{2+} > Na^+ = K^+$		leaf, root, CT	BS, MD, Grv	Glu, Ala, Asn, Gln, Cys, Gly, Ser, GSH	[23, 48, 51]
GLR3.4	$Ca^{2+} > Na^+$	PM, ~~T~~, ~~EM~~	leaf, stem, root, GC, CT	cold, NaCl, touch	Asn, Ser, Gly, Ala, Glu, ~~Gln~~, ~~Cys~~, ~~Asp~~	[48, 54, 55]
GLR3.5		PM, EM		$\downarrow\Psi_w$, MD	Met	[48, 51, 56]
GLR3.6	$Ca^{2+} > Na^+ = K^+$	PM	leaf, stem, root, CT	BS, MD	Glu	[23, 48,51, 57]
GLR3.7	Ca^{2+}	PM	leaf, stem, root	NaCl		[48]
CNGC1	Ca^{2+}, K^+, Pb^+, ~~Na^+~~, ~~Zn^{2+}~~, ~~Mn^{2+}~~, ~~Cd^{2+}~~		root, ~~leaf~~	HM		[58]
CNGC2	Ca^{2+}, Na^+, K^+	PM	leaf, CT, flower, root	BS, heating	cAMP, ATP	[58, 59]
CNGC3	K^+, Na^+	PM, ~~T~~	root, CT, LEAF, stem	NaCl	Na^+	[58, 60]
CNGC4	Ca^{2+}, Na^+, K^+			BS		[58]
CNGC5	Mg^{2+}, Ca^{2+}, Na^+	PM	leaf, root, GC		Hyp, cGMP	[61]
CNGC6	Mg^{2+}, Ca^{2+}, Na^+	PM	flower > leaves > > pods > root > > stem, GC	BS, heating	Hyp, cAMP, cGMP	[58, 61, 62]
CNGC7 CNGC8		PM	pollen			[63]
CNGC10	K^+, Na^+	PM, EM	root > leaf, mesophyll, epidermis	Grv, NaCl		[58, 64]
CNGC11 CNGC12	Ca^{2+}, K^+	PM		BS	cAMP, ~~cGMP~~	[65]

Table (*cont.*)

Channel	Selectivity	Cell localization	Tissue localization	Stimulus	Regulation	References
CNGC14	Ca^{2+}	PM	root	Grv	auxins, ~~ATP~~	[66, 67]
CNGC15	Ca^{2+}	PM, nucleus			NO_3^-	[67, 68]
CNGC16	Ca^{2+}		pollen	heating	cGMP	[69]
CNGC17		PM			cGMP	[70]
CNGC18	Ca^{2+}	PM	pollen		cAMP, cGMP	[58]
CNGC19	Ca^{2+}	T, PM, ~~EM~~	leaf, root, CT	BS, MD	Hyp, cAMP, DAMP	[55, 58, 71]
CNGC20		T, ~~EM~~	root, GC, flower, mesophyll	NaCl		[58]
ANN1	$Ca^{2+} := K^+ > Na^+$	PM, T, EM, Cyt	root, epidermis	NaCl, MD, cold, heat, ~~↓Ψ_w~~	$OH^{\cdot}$, H_2O_2, ~~MT~~	[72-77]
ANN2	Ca^{2+}	PM, Cyt	leaf, root, flower, hypocotyl, pods	↓Ψ_w, heating	~~CRY2~~	[72,74]
ANN3	Ca^{2+}	PM, Cyt	root, hypocotyl, cotyledons	↓Ψ_w, heating	~~CRY2~~	[74]
ANN4	Ca^{2+}, K^+	PM, EM	leaf, root, flower, stem	↓Ψ_w, NaCl, cold		[73, 76]
ANN5	Ca^{2+}?	PM, nucleus, Cyt	flower, pods, pollen, ~~root~~		$[Ca^{2+}]_{cyt}$	[78, 79]
ANN8		PM, ~~nucleus~~		↓Ψ_w, NaCl		[80]
TPC1	$Ca^{2+} \approx K^+ \approx Na^+$	T	leaf, CT, root, flower, epidermis, mesophyll	BS, NaCl	Dep, $[Ca^{2+}]_{cyt}$, $[Ca^{2+}]_{vac}$, ~~↓pH~~	[32, 45, 55, 81]
MCA1	Ca^{2+}	PM, ~~T~~, ~~EM~~	leaf, CT, stem, root, flower, pods, ~~epidermis~~	cold, ↓Ψ_w, Grv	MT	[82, 83]
MCA2	Ca^{2+}	PM, ~~T~~, ~~EM~~	leaf, CT, stem, root, flower, pods	cold, Grv		[82, 83]
OSCA1.1	$K^+ > Ba^{2+} \approx Ca^{2+} > > Na^+ = Mg^{2+} = Cs^+$	PM	leaf, root, flower, GC	↓Ψ_w	MT	[84]
OSCA1.3	Ca^{2+}	PM	GC	BS	DAMP	[85]
OSCA1.7	Ca^{2+}?			BS	DAMP	[85]
Piezo1	Ca^{2+}?	T	leaf, hypocotyl, root, CT	BS, touch	MT	[86, 87]
DEK1	Ca^{2+}	PM	epidermis		MT	[88]
MSL1	$Cl^- \approx K^+$	EM, ~~PM~~		heating, HM, ~~↓Ψ_w~~, ~~NaCl~~	MT	[55, 89]

Table (*cont.*)

Channel	Selectivity	Cell localization	Tissue localization	Stimulus	Regulation	References
MSL2 MSL3		EM, ~~PM~~		$\downarrow\Psi_w$		[90]
MSL4 MSL5 MSL6		PM	root		MT	[90]
MSL8	$Cl^- > Na^+$	PM, ~~ER~~, ~~T~~	pollen		MT	[45, 91]
MSL9	$Cl^- > Ca^{2+}$	PM, EM		$\downarrow\Psi_w$	MT	[90, 92]
MSL10	$Cl^- > Ca^{2+} \approx Na^+$	PM, EM	CT	$\downarrow\Psi_w$	MT	[90, 92-96]
SLAC1	Cl^-, NO_3^-		GC, hypocotyl	BS, $\downarrow\Psi_w$, dark	ABA, Ca^{2+}	[32, 97, 98]
SLAH1	Cl^-, NO_3^-		root			[32, 97, 98]
SLAH2	NO_3^-		root			[32, 34, 97, 98]
SLAH3	NO_3^-		root, leaf, GC		Dep, pH, ABA, NO_3^-	[32, 34, 97-99]
ALMT6	malate, fumarate > citrate, Cl^-, NO_3^-	T	leaf, GC, flower, ~~root~~		Ca^{2+}, pH, malate	[100, 101]
ALMT12/ QUAC1	malate and sulfate		GC		Dep, malate	[32, 98]
TMEM16A		EM			Ca^{2+}	[32, 102]
DTX33 DTX35		T	root, leaf, GC, flower, stem		pH	[103]
VCCN1	$Cl^- > NO_3^-$	EM	leaf, flower	light	Dep, ~~Ca^{2+}~~	[104]
GORK1	K^+, NH_4^+		root, GC, leaf	BS, NaCl, ROS	Dep, H_2O_2, ~~↓pH~~, ~~Hyp~~	[47, 105, 106]
SKOR	$K^+ > Na^+$		root, CT, ~~stem~~, ~~leaf~~		Dep, H_2O_2, $[K^+]_{in}$, ~~↓pH~~	[47, 107]
KAT1	K^+	PM, EM	GC	light	Hyp, ABA	[47, 108-110]
KAT2	K^+	PM	GC		Hyp, ~~↓pH~~	[47, 108, 109]
KC1	K^+	PM	root, 3K, leaf		~~↓pH~~	[47, 109]
AKT1	$K^+ > Na^+$	PM	root		Hyp, ~~↓pH~~	[47, 108, 109]
AKT2	K^+	PM	CT		Hyp, Ca^{2+}, cAMP, ~~↓pH~~	[47, 105, 109, 111]
TPK1	$K^+ > NH_4^+ \gg Na^+$	T	GC, root, mesophyll, CT, pollen	NaCl	$[Ca^{2+}]_{cyt}$, ABA, CO_2, ~~↓pH~~, ~~↑pH~~	[47, 112]

Table (*cont.*)

Channel	Selectivity	Cell localization	Tissue localization	Stimulus	Regulation	References
TPK4	$K^+ > NH_4^+ \gg Na^+$	PM	root, pollen		MT, ~~$\downarrow pH_{cyt}$~~, ~~$\downarrow \Psi W$~~, $[Ca^{2+}]_{out}$	[47, 113]
KCO3	K^+	T	leaf, stem, root, flower, CT	$\downarrow \Psi_w$		[47, 114]
SPIK	K^+	PM	pollen		Hyp, $\downarrow$pH	[47, 115]

Notes. Absence of the indicated selectivity, localization, etc., is marked with crossing out lines. Abbreviations: ABA, abscisic acid; PM, plasma membrane; T, tonoplast; EM, endomembrane; Cyt, cytosol; GC, guard cells, CT, conducting tissues; $\downarrow\Psi_w$, osmotic stress; BS, biotic stress; HM, heavy metals; MD, mechanical damage; Grv, gravitation; MT, membrane tension; Dep, depolarization; Hyp, hyperpolarization; DAMP, damage-associated molecular pattern.

in combination with localization, makes the channels from this group potential participants in generation of ES in higher plants.

CNGC are low-selective cation channels, which are structurally close to the discussed below shaker-like K^+-channels. For some CNGC activation with cyclic nucleotides such as cAMP and cGMP and with hyperpolarization has been established, which allows considering them as belonging simultaneously to the HACC and VICC groups [45, 55, 58]. CNGC are mainly located on plasmalemma, and also are present on the nuclear membrane and tonoplast. Many CNGC are tissue-specific and are mainly present in conducting tissues, epidermis, and guard cells [55, 58, 116]. Response to different stimuli and/or protective response to stressors including those inducing changes in electrical activity [3] due to salinization, drought, temperature change, pathogens, heavy metals, and others (table) was demonstrated for the channels from this group [55, 58, 67, 116]. Localization of CNGC on the plasma membrane of the cells in conducting tissues allows suggesting participation of some of the members of this family of channels in generation of ES in higher plants.

Annexins represent a group of cytoplasmic proteins capable of binding to phospholipids of plasmalemma, tonoplast, and ER membrane, they play a role of low-selective cation channels, probably belonging to the VICC group [45, 55]. The stimuli inducing activation of the channels from this family include drought, salinization, temperature change. ROS could play a role of annexin regulators (table), which, as have been mentioned above, could be inducers of VP [45, 55, 72-74].

TPCs are represented in Arabidopsis by a single gene *TPC1*, which is expressed in all plant tissues on the vacuolar membrane. TPC1 is a cation channel with low selectivity and slow activation kinetics with slight advantage for Ca^{2+} [55, 116]. It is known that TPC1 is activated by depolarization and cytosolic Ca^{2+} [45, 55]. TPC1 participates in the protective response to various stressors such as salinization, flooding, attacks of pests, etc., is associated with stomatal closure, hormonal regulation, and production of ROS through NADPH-oxidase [45, 55, 116], i.e., physiological processes regulation of which is realized through transmission of ESs [1, 2, 4, 5, 7]. Taking into account selectivity, localization on tonoplast, and mechanism of activation, TPC1 could be considered as a promising participant in ES generation.

Consideration of mechanosensitive Ca^{2+}-channels should begin with the *MCA* family [45, 55], which are localized on plasmalemma and expressed at especially high level in conducting tissues [55, 82, 90]. MCA are activated by the changes in membrane tension caused by osmotic stress, mechanical actions, cold, and other stimuli [82, 90, 116-118]. Permeability for Ca^{2+} and localization in conducting bundles allows considering this family of channels as the most probable participants in generation of ES among the mechanosensitive Ca^{2+}-channels.

OSCA1 are plasmalemma cation channels with low selectivity localized predominantly in the stomata guard cells [45, 55]. Their activation occurs during changes in membrane tension, they play a role of osmosensors and regulate stomatal closure, although some members of this family are, likely, activated by the damage-associated molecular patterns (DAMP), and indirectly participate in the protective response to attack of pathogens [55, 85]. Rather specific localization and functional role of the OSCA1 channels make them unlikely participants in electrical signaling.

Other mechanosensitive channels discovered in plants include the plant piezo channel Piezo1 and not related, but with electrophysiological characteristics similar to the mouse piezo channel, the RMA channel encoded by the *DEK1* (*DEFECTIVE KERNEL1*) gene from the family of phytocalpains. Both channels are fast activated and inactivated cation channels with low conductance [45, 55]. RMA is located predominantly on plasmalemma of epidermal cells and, most likely, is responsible for correct formation of epidermis and tissues underneath [95]. Piezo1 is localized primarily in the root cap, in conducting tissues, pollen, and in the pollen tube,

where it mostly detected on tonoplast. Its main functions are associated with mechanosensitivity of the roots in the solid substrate and antiviral immunity [86, 87, 119]. Limited amount of information on the channels Piezo1 and RMA available at present does not allow univocal conclusion on their possible role in generation of ES in plants.

In conclusion, it can be stated that the representatives from a number of Ca^{2+}-channels families potentially could participate in generation of ES in plants. Based on such criteria as localization, mechanism of activation, and functional role, the most probable candidates are the members of the GLR, CNGC, TPC1, MCA, and ANN families of channels.

Anion channels. Many anion channels in plants transmit not only chloride ions, but also other anions including nitrates, sulfates, and some organic anions. One important feature is the fact that under normal conditions intracellular concentration of anions are higher than extracellular, hence, concentration gradient is directed outward. Based on electrophysiological characteristics anion channels are commonly divided into two types: rapid, R-type, and slow, S-type. The former ones, R-type, are voltage-dependent, exhibit fast activation/deactivation (within milliseconds), and predominantly transport chlorides, nitrates, and sulfates, while the S-type channels are voltage-independent with activation/deactivation times around 10 s, exhibit high permeability for nitrates and lower permeability for all other anions [32, 34, 97, 98]. It is worth mentioning that such classification was suggested during investigation of anion channels in guard cells; later another types of anion channels have been discovered such as separately recognized aluminum-sensitive channels, mechanosensitive anion channels, and endomembrane anion channels [32, 34].

Mechanosensitive-like channels (MSL) exhibit, predominantly, anion permeability in higher plants, despite the traditional for many reviews attribution of MSL to Ca^{2+}-channels [45, 55]. Representatives of this family are localized mainly on plasmalemma and ER membrane (table). Many plasmalemma MSL channels have high tissue- and organ-specificity, and are expressed predominantly in roots, with exception of *MSL8*, which is expressed in pollen, and *MSL10*, which is strongly expressed in conducting tissues along with roots [45, 90, 94, 96]. MSLs are activated by changes in membrane tensions including during osmotic stress, and are characterized with relatively high conductance in comparison with other mechanosensitive channels [45, 55, 90, 94]. Majority of the members of MSL family, likely, cannot be assigned to the participants in ES generation due to their specific role and localization in roots. However, one of the members of the family, MSL10, required more detailed consideration as a potential participant in the mechanism of ES generation, because it meets the criteria: in addition to mechanosensitivity, selectivity to Cl^-, and localization on the plasma membrane of conducting cells, it is also capable of activating production of ROS with participation of NADPH-oxidase, operation of which, as mentioned above, could provide contribution to propagation of VP [55, 90, 94, 96, 116, 117].

Members of the family of slow anion channels (SLAC/SLAH, slow anion channel associated) belong to the S-type of channels localized on plasmalemma. There are differences between the members of the family: SLAH2 and SLAH3 predominantly transport nitrates and do not transport significant amounts of chlorides, while rest of the channels of the family transport both chlorides and nitrates [32, 34, 98]. There are also some differences in localization: SLAH1 and SLAH2 are predominantly expressed in roots, while expression of SLAC1 and SLAH3 is wider including in guard cells. Activation of SLAC1 could be triggered by various stimuli, and some of them cause changes in electrical activity such as attack of pathogens, increase of CO_2 concentration, drought, darkness, etc., likely via the Ca^{2+}-dependent pathway. SLAH3, in addition to Ca^{2+}-dependent regulation, could be activated by depolarization and acidification of cytosol [32, 34, 97-99]. Among the members of this family, SLAC1 and SLAH3 could be assigned to the group of potential participants in ES generation, because they meet all the criteria in selectivity and regulation.

Representative of the family of aluminum-activated malate transporters (ALMT) encoded by the *ALMT12* gene was identified as an R-type channel. Another name of ALMT12 – quickly activating anion channel 1 (QUAC1) has been given to this channel due to the absence of activation of this channel by aluminum typical for other members of this family [32, 34]. The QUAC1 channel is localized on plasmalemma of guard cells and participates in stomatal closure, it is activated by depolarization, exhibits activation/deactivation times characteristic for R-type of channels, and transports malate and sulfate. Another member of the family, ALMT6, which is localized on tonoplast, exhibits predominantly malate and fumarate permeability, but also transports chloride, it is activated by Ca^{2+} and acidic pH in vacuole [100, 101]. Other well investigated at present representatives of ALMTs are localized mainly in roots, and, most likely, are activated through the aluminum-dependent pathway [32, 34, 98]. Based on the electrophysiological characteristics, among the members of ALMT family only QUAC1 could be considered as a potential participant in ES generation, however, available at the moment information on its localization contradicts this assumption.

Among the other anion channels, representatives of the family of detoxification efflux carriers (DTX), DTX33 and DTX35, localized on tonoplast in many plant tissues should be mentioned. These channels are responsible for the voltage-dependent influx of chloride

and other anions to vacuole controlled by pH changes [103]. The protein localized on the ER membrane and encoded by the *TMEM16* gene could, potentially, function as a Ca^{2+}-activated anion channel [32, 102]. There is also information on the voltage-dependent Cl^- channel 1 (VCCN1) in thylakoids, which is activated by depolarization and light, but not by Ca^{2+}, and participates in regulation of photosynthesis [104].

Hence, from the point of view of potential participation in generation of ES, most attention should be paid to the following anion channels: MSL10, QUAC1, SLAC1, and SLAH3.

Potassium channels. The most detailed analysis of electrophysiological characteristics of the channels and the genes coding for these channels has been performed for the K^+-channels. The main principle of classification of K^+-channels is based on the mechanism of activation and type of observed permeability [35, 46, 47]. Based on the mechanisms of activation the channels are divided into voltage-dependent and voltage-independent channels. The voltage-dependent K^+-channels are localized on plasmalemma, while the voltage-independent, with some exception, are endomembrane K^+-channels [46, 47]. The voltage-dependent K^+-channels are sub-divided into the channels mediating potassium efflux (K^+_{out}) and influx (K^+_{in}), and sometimes the channels with weak permeability (K^+_{weak}) are identified among the latter [35, 46, 120].

Currently two families of the K^+-channel genes have been recognized: Shaker-type K^+-channels and two-pore K^+ channels (TPK). All members of the Shaker-type K^+-channel family belong to the voltage-dependent channel, and, in turn, are subdivided into efflux channels (GORK, SKOR) and influx channels (AKT, KAT) [46]. Sometimes among the genes of K^+_{in}-channel the *KC1* gene (*KAT3*), which codes for the regulatory subunit not capable of forming the channel on its own, but capable of affecting the K^+_{in}-channel characteristics by binding to them, is considered separately [46, 109]. All other genes of the Shaker-type K^+_{in}-channels [*KAT1*, *KAT2*, *AKT1*, *AKT2*, *AKT5*, and *SPIK* (*AKT6*)] code for the subunits that form channels; these channels are formed by either homomers or heteromers, and have slightly different electrophysiological characteristics [47, 108]. All channels in this subgroup are activated by hyperpolarization and generate inward K^+ flows with exception of AKT2, which is also capable to perform function of efflux channel [109, 111], and which is often assigned to the separate subgroup K^+_{weak} [46, 47, 120].

Two types of K^+_{out}-channels of the Shaker type have been identified in plants: GORK (guard cell K^+ outward rectifying channel) and SKOR (Shaker-type K^+ outward rectifying channel), both are activated by depolarization. Moreover, their activation could occur also with participation of Ca^{2+}-dependent protein kinases, as well as of ROS, which indicates possible involvement of these channels in generation of ES. However, it should be mentioned that *SKOR* is practically not expressed outside of roots (table), hence, the possibility of its participation in generation of ES in shoots is rather low, unlike for the widely expressed *GORK* [46, 47, 120].

TPK (KCO K^+ channel, outward rectifying) include voltage independent channels localized on tonoplast with exception of TPK4 localized predominantly on the pollen plasmalemma [46, 47]. Activation by Ca^{2+} and acidification of cytosol (pH 6.7 with normal pH level 7.5-7.8) was demonstrated for TPK1, this channel is responsible for release of vacuolar K^+ during, for example, stomatal closure. There is also data that these channels could be mechanosensitive responding to the changes of tonoplast curvature as osmosensors. As to plasmalemma-localized TPK4, it is pH-insensitive and can be blocked by the extracellular Ca^{2+} [47, 90, 112, 117].

Hence, among the currently known K^+-channels, only GORK and TPK1 could be considered as potential participants in ES formation in higher plants.

PARTICIPATION OF ION CHANNELS IN ELECTRICAL SIGNALING

Before starting discussion of the currently available proofs of participation of the genetically identified ion channels in generation of ES, some methodological limitations of such studies should be briefly considered. The main approach in such studies is the use of mutant plants deficient in the gene of interest or with its overexpression. Parameters of ES in these plants (amplitude, duration, peculiarities of propagation, and others) are next compared with the ES parameters determined for the wild type plants (Fig. 2). Presence of differences is considered as an indication of participation of this ion channel in the processes of generation and propagation of ES [20, 53, 93, 121]. In addition to the direct comparison of the ES parameters, simultaneous monitoring of the changes in concentrations of ions mediated by these channels could be also used, which could be followed by comparison of the type of these changes between the plant variants and with the ES parameters [23, 53, 122]. Moreover, artificial activation or deactivation of the particular channels by their specific ligands that cause typical changes of membrane potential could also be considered as a proof of participation in electrical signaling, however, such approach is applicable only to the ligand-activated channels [23, 123]. The abovementioned methods also have drawbacks. One of such drawbacks is possible interaction of the subunits encoded by different genes leading to formation of fully functional heteromeric channel, while the possibility of formation of homomeric channels also exists. Characteristics and functional roles of homo- and heteromeric channels could be different [47, 109, 124]. Investigation of the

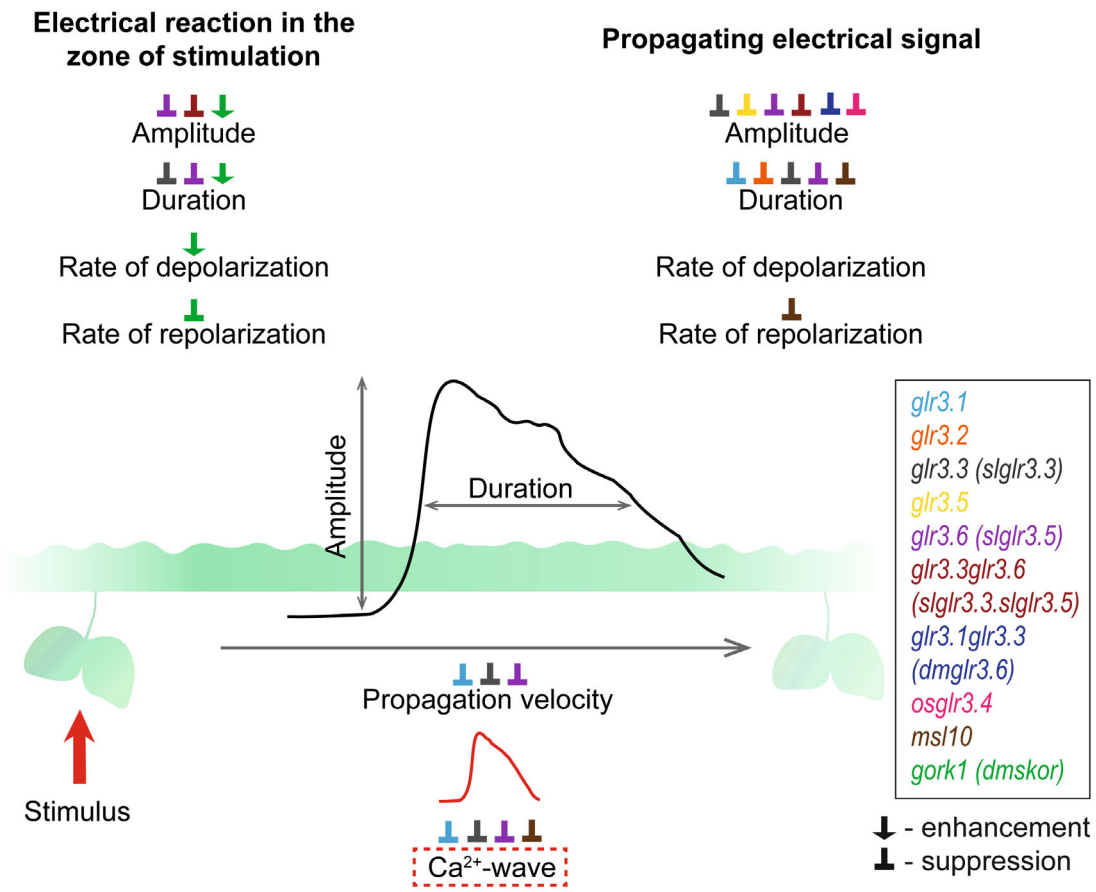

Fig. 2. Schematic representation of the effects of knockout mutations of the genes of ion channels on parameters of electrical signals and Ca^{2+} wave in higher plants. Membrane potential is shown as a black line, and Ca^{2+} wave – as a red line. Color of symbols indicated type of knockout mutation (see explanations in the text).

double- and more mutants also could not provide as unambiguous answer whether the change of ES parameters is associated with the fact that certain heteromeric channels are not formed, or some of the homomeric channels participating in generation of ES are suppressed [20, 53, 122].

Existence of a compensatory mechanism in the case of participation of several channels in generation of ES, when dysfunction of the suppressed gene is compensated by overexpression of another gene that perform the same or similar role, also could complicate interpretation of the results [77]. And finally, it was shown for some channels that they are capable to perform some of their functions, such as regulation of cell death, through their non-channel subunits [125]. Hence, the use of mutants does not provide an unambiguous answer, but at present there is no other approach for analysis of electrophysiological and molecular genetics data at the level of whole organism.

The most investigated participants of ES generation in plants are Ca^{2+}-channels, primarily from the GLR family (Fig. 2) [51]. Complete suppression of VP propagation outside of the region of the leaf subjected to mechanical damage [20, 21, 53, 56, 122], attack of chewing insects [20], excessive light [122], and laser-initiate damage [53] was observed in the *glr3.3glr3.6* double mutant of Arabidopsis. In the process, amplitude of electrical response decreases in the damaged leaf, but is not completely suppressed [20, 21, 56]. Mechanical damage of roots also causes decrease of amplitude and duration of ES in the leaves of the *glr3.3glr3.6* plants in comparison with the wild type plant [23]. In the case of single mutants, *glr3.3* or *glr3.6*, decrease of amplitude and duration of the propagated VP is observed [20, 53, 122]. It is worth mentioning that while in the case when in the VP induced by the leaf cutting there is a fast AP-like component in addition to the slow wave of depolarization, in the *glr3.6* mutant only the latter is suppressed [56]. With regards to the GLR3.3 channel, this channel in comparison with the GLR3.6, likely, provides larger contribution to the response to thermal stress, because in the *glr3.1glr3.3* double mutant the response to laser-induced burn is also completely suppressed, but not the response to mechanical damage [53]. It is important to note that during comparison of the *glr* mutant with the wild type coordinated changes were observed during simultaneous recording of the dynamics of Ca^{2+} concentration and dynamics of electric potential:

in the mutant forms with GLR deficit both Ca^{2+}-wave and VP were suppressed [23, 53, 122]. This indicates direct association between the changes of Ca^{2+} concentration mediated by the GLR channels and generation of VP.

In a number of studies artificial activation of GLR channels by addition of glutamate have been performed, which resulted in both increase of Ca^{2+} concentration in cytosol [57] and generation of ES [23]. Moreover, addition of glutamate to the mutant plants *glr3.3* and *glr3.6* practically did not induce either increase of Ca^{2+} or generation of ES [23, 57]. These data together with consideration of the temporal-spatial dynamics of Ca^{2+} concentration allow suggesting potential participation of GLR3.3 and GLR3.6 in the long-distance reaction to touch [126] and attack of aphids [121], and participation of GLR3.3 in the reaction to salt stress [127].

The data obtained for the tomato plants (*Solanum lycopersicum* L.) also indicate that GLRs play a role in generation of ES: complete suppression of VP transmission into the neighboring leaves was observed in the *SlGLR3.3* and *SlGLR3.5* (homologs of *GLR3.3* and *GLR3.6* in Arabidopsis) double mutants, while in the stressed leaf itself there was only reduction of amplitude [128].

Predominant expression of *GLR3.3* and *GLR3.6* in conducting bundles provides additional support to the suggestion that these channels participate in the systemic propagation of ESs. In particular, pronounced expression has been detected in the primary, secondary, as well as tertiary bundles in the Arabidopsis leaves. It must be mentioned that *GLR3.3* is expressed mainly in the primary conducting bundles of phloem, while *GLR3.6* – in xylem [53, 57].

It was shown for other potential candidates from this family, that decrease of amplitude and duration of ES induced in response to mechanical or laser damage occurs in the *GLR3.1* and *GLR3.2* mutants [20, 53], however, even in double mutants, with exception of the previously mentioned *glr3.1glr3.3*, neither systemic reaction nor local reaction were suppressed completely [53]. It has been suggested that GLR3.1 participates in propagation of ES outside the limits of conducting bundles due to disruption of the ES-associated radial propagation of the Ca^{2+} signal [53]. The channels encoded by *GLR3.5* could be responsible for formation of the AP-like shape of ES in response to mechanical damage, however, the issue could be more complicated. In particular, in the mutant plants no AP-like shape of ES was observed in the non-stressed leaves, which have direct connection with the stressed leaf, unlike in the wild type plants, but it was present in the non-stressed leaves with indirect connections with the stressed leaf, in which the AP-like shape was absent in the wild type plant [56]. This provides another indication of complexity and versatility of the processes of generation and propagation of ESs in plants, which remain to be elucidated.

The DmGLR3.6 channel of the Venus flytrap, homolog of the Arabidopsis GLR3.1/3.3, potentially could participate in propagation of AP induced by touch from the trigger hair to the leaf of the trap, as evidenced by the specific pattern of expression of this gene and possibility of AP induction by glutamate in the leaf-trap [129, 130]. In monocots, such as rice (*Oryza sativa* L.), the gene *OsGLR3.4*, which encodes Ca^{2+}-channel with functions similar to the functions of GLR3.3 and GLR3.6 of Arabidopsis could be highlighted among the *GLRs*: systemic propagation of VP induced by mechanical damage is partially suppressed in the rice mutants deficient in this channel, while the local electrical response is not suppressed [123]. It is also worth mentioning that the channel OsGLR3.4 could be activated by several amino acids [123], unlike the glutamate-specific GLR3.3 and GLR3.6 in Arabidopsis [23], which could be due to the fact that from phylogenetic point of view *OsGLR3.4* is located at a relatively long distance from *GLR3.3* and *GLR3.6* [131].

Another type of channels for which their participation in formation of ES was determined using molecular genetics approach, are anion channels belonging to the family of mechanosensitive channels MSL (Fig. 2). In the *msl10* mutant plants reduction of the duration of the systemically transmitted VP induced by mechanical damage has been observed, which occurred due to disappearance of the phase of "slow depolarization" in VP, as indicated by the authors. VP in the *msl10* mutant plants demonstrated similarity of its characteristics with the VP in the *glr3.3* and *glr3.6* single-mutant plants. At the same time, no changes in the VP parameters have been revealed for the other mutants of *MSL* family, *msl4*, *msl5*, *msl6*, and *msl9* [93]. As has been mentioned above, expression of *MSL10* is observed in the conducting bundles including both phloem and xylem. The MSL10 channel demonstrates anion conductance, but not calcium conductance [93, 132]. Nevertheless, functioning of MSL10, most likely, activates influx of Ca^{2+} into the cell during mechanical damage through GLR3.3 and GLR3.6. It was demonstrated also that the initial depolarization phase occurs before the start of the changes in Ca^{2+} concentration [93], which raises the question regarding the accepted mechanism of VP generation.

And, finally, a channel has been identified ensuring K^+ flow in the course of AP depolarization phase – GORK1. Amplitude and rate of depolarization induced by the AP electric current in the *gork1* mutants was higher in comparison with the wild type, while repolarization was significantly slower (Fig. 2). The following mathematical modeling confirmed participation of this channel in generation of AP. It was also shown that GORK1 is activated already at the phase of depolarization decreasing its rate and amplitude under normal conditions [105]. It was also demonstrated in this study that another K^+-channel, AKT2, could affect generation of AP,

but not directly through regulation of the plasmalemma excitability [105].

Participation of two K^+-channels, DmSKOR belonging to the same group as the previously considered GORK1and KDM1, homolog of the KAT1 of Arabidopsis, was demonstrated in the recent studies on Venus flytrap [37, 129]. Suppression of the *DmSKOR* expression by coronatine, which suppresses expression of the genes associated with excitability in Venus flytrap, resulted in the increase of the time of repolarization during generation of the mechanically induced AP in the trap leaf, which could indicate participation of DmSKOR in formation of depolarization phase in AP [129, 130]. KDM1 is a channel activated by hyperpolarization and acidic pH of apoplast, which is localized exclusively in the mechanosensitive hairs and responsible for the K^+ influx into the cell. Mathematical modeling and comparison with the experimental data showed that the role of this channel involves restoration of K^+ concentration during generation of a series of APs resulting in the trap closing in Venus flytrap and initiation of the release of digestive enzymes [37].

Potential contribution of certain channels to generation of ES could be suggested not only based on the effects of mutation on parameters of ES *pre se*, but also based on their effects on parameters of Ca^{2+}-signals, because there is close similarity between the dynamics of Ca^{2+} concentration and dynamics of the changes of electric potential during excitation [53, 129]. In particular, decrease of amplitude and of the rate of Ca^{2+} wave in response to salinization [81, 133] and mechanical damage [134] was observed in the vacuolar channel TPC1 mutants. In the case of attack of aphids, overexpression of *TPC1* results in systemic increase of Ca^{2+}, which is not observed in the wild type [121]. Nevertheless, the authors suggested only auxiliary role of TPC1 in initiating response to salinization and mechanical damage involving enhancement of the Ca^{2+} concentration shift initiated by other channels [133, 134]. The demonstrated role of TPC1 in formation of Ca^{2+}-wave induced by different stimuli together with the presumed role of tonoplast in ES generation [44], and taking into consideration the data of inhibitory analysis [15, 42] allows suggesting direct involvement of TPC1 in generation of ES. Contribution to formation of Ca^{2+}-signal was also demonstrated for the channel from a different family, CNGC19, localized on the plasmalemma of phloem cells: participation of the channel in the increase of Ca^{2+} concentration in response to the attack of chewing insect was revealed, moreover, activation of CNGC19 could be mediated by either Pep1 (Protein elicitor peptide 1, one of the DAMP released during the cell damage) or directly by cAMP, content of which also increases during the damage [71].

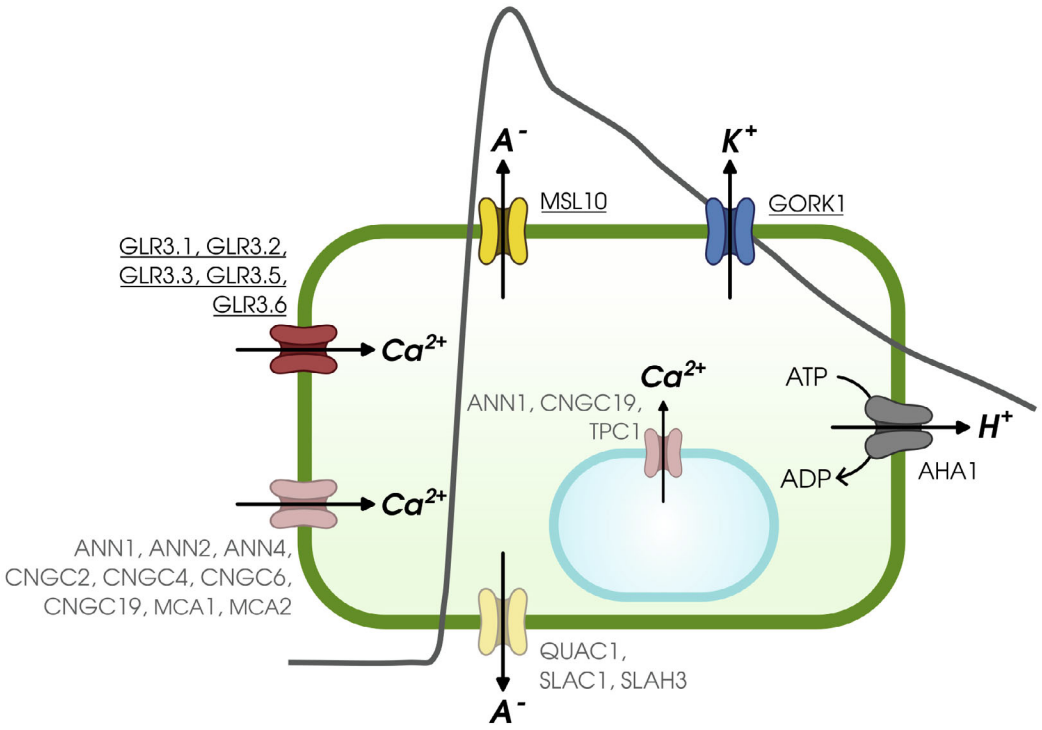

Fig. 3. Ion channels participating in generation and propagation of electrical signals (ES) in a cell of higher plants. Location of ion channels corresponds to particular phase of the process of ES generation to which their contribute, which exception of Ca^{2+}-channels, which could be activated at different stages of the process of ES formation. Ion channels with experimentally proved participation in ES generation are underlined. Ion channels, which, potentially, could participate in generation of ES are shown in regular font. The H^+-ATPase, AHA1, that also provides contribution to generation of ES is shown in the figure [2, 7].

In addition to the results of investigating propagating Ca^{2+}-signal, data on the changes of Ca^{2+} concentration in the zone of stimulus action exemplified, in particular, by the well investigated stimuli such as heating and cooling, could be also used. The studies with *MCA1* and *MCA2* [118], *ANN1* and *ANN4* [73], *OsCNGC14* and *OsCNGC16* (homologs of *CNGC*2 and *CNGC4* in Arabidopsis) [135] mutants demonstrated decrease of the amplitude of Ca^{2+} increase in cytosol induced by cold in comparison with the wild type plants. Moreover, the amplitude also decreases under the action of inhibitors suppressing AP, which together with the characteristic shape of Ca^{2+}-signal allows suggesting participation of these channels in generation of electrical response in the zone of cooling [73, 118, 135]. It should be mentioned that the increase of Ca^{2+} concentration was not completely suppressed in any of the mutants including the double ones [118]. Moreover, if the degrees of reduction of calcium concentration observed for different mutants are summarized, the resulting degree is much higher than 100%, which, obviously, indicates either compensatory expression of other genes, or existence of different participants in the processes of changing Ca^{2+} levels in different plant species [73, 118, 135]. Suppression of the Ca^{2+} wave in cytosol induced by another well investigated stimulus, heating, was shown in the *CNGC2*, *CNGC6*, *OsCNGC14*, *OsCNGC16*, *ANN1*, and *ANN2* mutant plants; furthermore, the heating-induced increase of Ca^{2+} level in the wild type plants is similar to the VP in shape and duration [62, 72, 135, 136]. The abovementioned information implies that the discussed channels could provide contribution to generation of electrical response in the zone of the corresponding stimulus action.

In general, it could be stated with confidence that the following Ca^{2+}-channels in higher plants are involved in generation of propagating ES: GLR3.1, GLR3.2, GLR3.3, GLR3.5, and GLR3.6, as well as anion channel MSL10 and K^+-channel GORK1 (Fig. 3). The Ca^{2+}-channels ANN1, ANN2, ANN4, CNGC2, CNGC4, CNGC6, CNGC19 could be also considered as potential participants in generation of ES, as well as the vacuolar channel TPC1 and mechanosensitive channels MCA1 and MCA2. There are no experimental data supporting participation of anion channels QUAC1, SLAC1, and SLAH3 in this, but their properties indicate the possibility of their potential involvement in generation of ES.

CONCLUSIONS

In conclusion of our analysis of molecular mechanisms of electrical signaling in higher plants, it must be mentioned that further detailed investigations are necessary. Most significant results could be expected if the efforts are concentrated on the following issues: (i) identification of molecular nature of the voltage-dependent Ca^{2+}-channels of plasmalemma responsible for initiation of AP appearing in plants when the threshold level of depolarization is reached [8]; (ii) search for the genes encoding ion channels in different species of plants including the ones with locomotion and carnivorous plant, for which electrophysiological examinations are common. At the same time, investigation of the whole complexity of electrical signaling in plants is necessary, both from the point of view of different types of ES, and from the point of view of peculiarities of electrical signaling in different plant species. Best results could be achieved by combining electrophysiological and genetic approaches in a single study supplementing them with analysis of ion concentration in intact plants using, for example, genetically encoded fluorescent sensors.

Identification and characterization of ion channels participating in generation of ES could provide significant contribution not only to elucidation of mechanisms of excitation in plants but also to the general picture of the functional role of ES, because induction of functional response to the propagating ES is based on the changes of ion concentration in the cells and tissues caused by propagation of ES [5, 6]. In future it would facilitate resolving such important issues such as possibility of information transmission with participation of ES in plants [3] and interaction of electrical signaling system with other types of signalling systems such hormonal, calcium, and ROS [1, 2, 4, 7].

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