

Mathematical Models of Electrical Activity in Plants

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Abstract Electrical activity plays an important role in plant life; in particular, electrical responses can participate in the reception of the action of stressors (local electrical responses and oscillations) and signal transduction into unstimulated parts of the plant (action potential, variation potential and system potential). Understanding the mechanisms of electrical responses and subsequent changes in physiological processes and the prediction of plant responses to stressors requires the elaboration of mathematical models of electrical activity in plant organisms. Our review describes approaches to the simulation of plant electrogenesis and summarizes current models of electrical activity in these organisms. It is shown that there are numerous models of the generation of electrical responses, which are based on various descriptions (from modifications of the classical Hodgkin–Huxley model to detailed models, which consider ion transporters, regulatory processes, buffers, etc.). A moderate number of works simulate the propagation of electrical signals using equivalent electrical circuits, systems of excitable elements with local electrical coupling and descriptions of chemical signal propagation. The transmission of signals from a plasma membrane to intracellular compartments (endoplasmic reticulum, vacuole) during the generation of electrical responses is much less modelled. Finally, only a few works simulate plant physiological changes that are connected with electrical responses or investigate the inverse problem: reconstruction of the type and parameters of stimuli

through the analysis of electrical responses. In the conclusion of the review, we discuss future perspectives on the simulation of electrical activity in plants.

Keywords Electrical signals · Simulation of plant electrical activity

Introduction

The perception of information about environmental factors is a necessary mechanism for a plant adaptation. The plasma membrane plays a key role in this perception, and the generation of electrical responses (changes in the gradient of electrical potential on the plasma membrane) is an important part of a plant's early response to external stimuli. Changes in the activities of ion channels (Trebacz et al. 2006; Fromm and Lautner 2007; Felle and Zimmermann 2007) and systems of active transport (Hills et al. 2012) are the main mechanisms of the generation of electrical response. Initial shifts in the membrane potential (Oprittov et al. 1991, 2005), the activation of signalling cascades in the plasma membrane (Nayyar 2003; Gilroy et al. 2016) and/or modification of their properties (fluidity, surface charge, electrostriction) (Hauser et al. 1976; Oprittov et al. 1991; Pyatygin et al. 1992; Murata and Los 1997) can participate in the development of these changes due to external stimuli.

Stimulus-induced electrical responses can cause physiological changes in the stimulated zone (Pyatygin 2004) and the propagation of electrical signals (ESs) through the plant body (Sibaoka 1991; Trebacz et al. 2006; Beilby 2007; Fromm and Lautner 2007; Gallé et al. 2015; Vodenneev et al. 2015; Sukhov 2016). The ESs can induce the movement of organs in some plants including the pulvinus

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in *Mimosa pudica*, the trap lobes in *Dionaea muscipula* and *Aldrovanda vesiculosa*, and the tentacle in *Drosera* (Sibaoka 1991). In addition, the ESs, which propagate from stimulated zone to unstimulated parts of the plant, induce numerous physiological changes in these parts (Fromm and Lautner 2007; Gallé et al. 2015; Sukhov 2016). The responses include respiratory activation (Filek and Kościelniak 1997; Lautner et al. 2014), shifts in transpiration rate and stomata opening (Fromm and Fei 1998; Grams et al. 2007), changes in photosynthetic activity (Fromm and Fei 1998; Krupenina and Bulychev 2007; Pavlovič et al. 2011; Grams et al. 2009; Sukhov et al. 2012, 2014a, 2015a, 2016; Sherstneva et al. 2015), increased ATP content in leaves (Surova et al. 2016b), modification of the consumption of mineral compounds by roots (Oprítov et al. 1991; Shabala and Knowles 2002), suppression of phloem transport (Fromm 1991; Fromm and Bauer 1994; Furch et al. 2010), stimulation of the expression of defence genes (Graham et al. 1986; Fisahn et al. 2004; Mousavi et al. 2013), the production of phytohormones (Dziubinska et al. 2003; Hlavinka et al. 2012), and the cytoplasmic streaming cessation in the characean algae (Williamson and Ashley 1982). It is probable that the result of these physiological changes led to the evolution of plant adaptation to negative environmental conditions (Retivin et al. 1997, 1999; Sukhov et al. 2014b, 2015b; Surova et al. 2016a; Sukhov 2016).

Investigation of the mechanisms of generation of stimulus-induced electrical responses and ES propagation is necessary to understand the mechanisms of physiological changes and adaptation. The simulation of electrophysiological processes in plant cells is a prospective tool for theoretical investigation of the problem (Beilby 1981, 1982, 2007; Beilby and Al Khazaaly 2016; Mummert and Gradmann 1991; Sukhov and Vodeneev 2009; Hills et al. 2012; Sukhov et al. 2013; Chatterjee et al. 2014). There are a number of benefits of simulation: rapid testing of hypotheses about the mechanisms of investigated processes, prediction of the plant response that can be used to improve the design of future experiments, improvement of the interpretation of experimental results, etc. These benefits are especially important for the investigation of complex processes in plant electrophysiology, including multi-cellular interactions among plant cells (e.g. ES propagation, Sukhov et al. 2011a), the cooperative activity of ion-transport systems in the cells (e.g. electrical oscillations, Gradmann 2001a, b), the development of various physiological changes connected to ion transport and electrical activity (e.g. closing/opening of stomata, Chen et al. 2012), and others.

There are two main ways to simulate electrical activity in plants. (i) Elaboration of detailed mathematical models of the reception of stimuli of plant cells (including

responses to salinity in salt tolerant and salt sensitive plants, electrical current, and cooling), generation of electrical responses, propagation of ESs and development of physiological changes (Beilby 1981, 1982, 2007; Mummert and Gradmann 1991; Gradmann 2001a, b; Garkusha et al. 2002; Sukhov and Vodeneev 2009; Sukhov et al. 2011a, 2013; Chen et al. 2012; Beilby and Casanova 2014; Minguet-Parramona et al. 2016; Beilby and Al Khazaaly 2016), considering the mechanisms of the investigated processes. This approach is the basis of theoretical testing of different mechanistic hypotheses about the mechanisms of these processes. (ii) The use of regression equations (or neural networks) to describe the connection between stimulation ('input') and the plant electrical response ('output') (Chatterjee et al. 2014, 2015; Chen et al. 2016). This approach can be used to predict the plant response to external stimuli and to detect stimulus parameters based on the characteristics of electrical response. The aim of our work is to review the modern mathematical models of both groups.

Electrical Responses of Plants and Their Mechanisms

It is well known that the stimulation of plant cells changes the activities of ion transporters in the plasma membrane and induces electrical responses. There are several types of electrical responses in plants, including local electrical responses (LERs) of cells in the zone of stressors action (Krol and Trebacz 1999; Oprítov et al. 2005; Vodeneev et al. 2015), action potential (AP) (Trebacz et al. 2006; Fromm and Lautner 2007; Gallé et al. 2015), variation potential (VP) (Stahlberg et al. 2006; Vodeneev et al. 2015), and system potential (SP) (Zimmermann et al. 2009, 2016). In addition, plants have periodic electrical oscillations that can participate in the reception of stimuli (Shabala et al. 2006).

Local electrical responses are generated by plant cells in the zone of stimulation under the action of various factors (cooling, touch, changes in illumination, and others) (Bulychev and Vredenberg 1995; Trebacz and Sievers 1998; Pikulenko and Bulychev 2005; Oprítov et al. 2005; Krol et al. 2003, 2006). Their amplitude is somewhat dependent on the intensity and duration of the stimulus. In some cases, LERs can induce propagating ESs, e.g. action potential (Trebacz and Sievers 1998; Pikulenko and Bulychev 2005; Oprítov et al. 2005). It is probable that the transient inactivation of H^+ -ATPase, which is the main active electrogenic transporter of the plasma membrane, is the important mechanism of LER generation (Oprítov et al. 2005). It is known that inactivation of this transporter can be induced by low temperature (Pyatygin 2004; Oprítov et al. 2005)

and changes in light intensities (Bulychev and Vredenberg 1995; Pikulenko and Bulychev 2005). The recovery of H^+ -ATPase activity causes repolarization of the plasma membrane (Bulychev and Vredenberg 1995). Another important mechanism of LERs is changes in the activities of ion channels, which were observed after stimulation by cold (Krol et al. 2003, 2004), light (Krol and Trebacz 1999) or osmotic stress (Shepherd et al. 2008).

AP is an electrical signal consisting of a short-term spike of electrical potential on the plasma membrane (Fig. 1a). AP operates under an all-or-none law, i.e. subthreshold stimuli do not induce AP, and overthreshold stimuli cause a signal with constant amplitude (Trebacz et al. 2006). The classical scheme of AP generation (Trebacz et al. 1989, 2006; Beilby 2007; Felle and Zimmermann 2007; Fromm and Lautner 2007) in plants (*Charophyceae*, liverworts, higher plants) is based on the following chain of events: stimuli—initial depolarization—activation of potential-dependent Ca^{2+} channels in plasma membrane and, possibly, inositol-3-phosphate (IP_3)-dependent Ca^{2+} channels in intracellular compartments (endoplasmic reticulum, vacuole)—increase in concentration of calcium ions in cytoplasm—activation of Cl^- channels—depolarization of electrical potential on plasma membrane—activation of outward K^+ channels—repolarization. Higher plants have an additional mechanism of AP generation (Vodeneev et al. 2006, 2015; Sukhov 2016), namely a transient inactivation of H^+ -ATPase caused by the transient increase in calcium concentration. An alternative mechanism of AP generation has been shown in the green algae *Acetabularia* (Gradmann 1976), which are in a very different branch of plant lineage; the mechanism is

connected with a transient inactivation of the chloride electrogenic pump. AP is a self-propagating ES (Trebacz et al. 2006; Beilby 2007; Krol et al. 2010). In lower plants, AP propagates through a homogeneous symplast of cells of the plant body (Trebacz et al. 2006); in higher plants, action potential propagates through a symplast of sieve elements and (or) a symplast of parenchyma cells (Oprittov et al. 1991; Fromm and Lautner 2007; Zhao et al. 2015; Vodeneev et al. 2016) in vascular bundles.

VP is a long-term electrical signal induced by various types of damage (burning, heating, mechanical wounding, etc.); it has an irregular shape (Fig. 1b), including long-term depolarization and short-term ‘AP-like’ spikes (Stahlberg et al. 2006; Vodeneev et al. 2015; Sukhov 2016). It is possible that variation potential is a local electric response to the propagation of a non-electrical signal (Vodeneev et al. 2015) because VP amplitude is dependent on the parameters of damage, and the signal propagation is not electrotonic. The probable routes of VP propagation include transmission of a chemical signal (Rhodes et al. 1999; León et al. 2001), a hydraulic wave (Mancuso 1999; Stahlberg et al. 2006) or their combination (Malone 1994; Vodeneev et al. 2015), activating mechanosensitive and/or ligand-dependent Ca^{2+} channels (Vodeneev et al. 2015; Sukhov 2016). Ca^{2+} influx induces the inactivation of H^+ -ATPase and the activation of Cl^- channels that cause the depolarization of the plasma membrane (Stahlberg and Cosgrove 1997; Vodeneev et al. 2011, 2015; Katicheva et al. 2014). The inactivation of H^+ -ATPase is the main mechanism of long-term depolarization (Katicheva et al. 2014; Vodeneev et al. 2015); the inactivation may be caused by a long-term activation of Ca^{2+} channels (Katicheva et al. 2015). However, a short-term activation of Cl^- channels is a possible mechanism of ‘AP-like’ spikes (Katicheva et al. 2014; Vodeneev et al. 2015).

SP is a propagating electrical signal that represents a transitory hyperpolarization (Zimmermann et al. 2009, 2016) (Fig. 1c). System potential is caused by the activation of H^+ -ATPase (Zimmermann et al. 2009). It is also probable that the signal is connected to K^+ channels because preliminary blocking of these channels suppresses the propagation of the hyperpolarization signal (Lautner et al. 2005), and the inactivation of K^+ channels induces the activation of H^+ -ATPase (Sokolik et al. 2001).

Oscillations of membrane potential and ion fluxes can be induced in plants by the action of light (Shabala and Newman 1999), root nutrition (Shabala and Knowles 2002), salt stress (Shabala 2000), the development of turgor pressure in the stomata (Gradmann et al. 1993), changes in the diver depth of algae (Gradmann and Boyd 1995), etc. The mechanism of electrical oscillations is connected to changes in the activities of H^+ -ATPase, $2H^+/Cl^-$ symporter, K^+ , Cl^- and Ca^{2+} channels as well as interactions

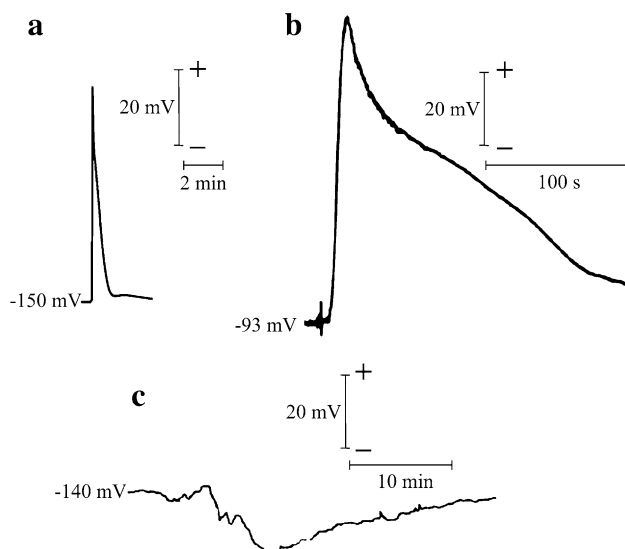


Fig. 1 Electrical signals in plants. **a** Action potential (Krol et al. 2004); **b** variation potential (Katicheva et al. 2014); **c** system potential (Zimmermann et al. 2009)

of these transporters (Shabala 2000, 2003; Shabala and Knowles 2002; Shabala et al. 2006).

Thus, electrical responses (LERs, ESs, electrical oscillations) have complex mechanisms that require detailed investigations. The simulation of different processes in plant electrogenesis is an important method in these investigations (Gradmann 2001a; Sukhov and Vodeneev 2009; Minguet-Parramona et al. 2016). The elaboration of mathematical models of electrical responses and their analysis can be used to investigate the mechanisms of electrical activity and their physiological effects.

Basic Approaches to Description of Electrical Response Generation in Plants

Describing the dynamics of membrane potential is the first step in the detailed simulation of the generation of electrical responses. In most works (Beilby 1981, 1982; Mummert and Gradmann 1991; Gradmann et al. 1993; Gradmann 2001a, b; Sukhov and Vodeneev 2009; Beilby and Al Khazaaly 2016; Novikova et al. 2017), Eq. (1) from the Hodgkin–Huxley model (Hodgkin and Huxley 1952) was used:

$$\frac{dE_m}{dt} = \frac{1}{C} F \sum_{r=1}^N z_r j_r, \quad (1)$$

where E_m is the membrane potential, C is the specific capacity of the biological membrane, F is the Faraday constant, N is the number of electrogenic transporters that participate in the electrical response, j_r is the specific flux from the transporter r , and z_r is the charge that the transporter r transfers per catalytic cycle. In some works (Sukhov et al. 2011a, 2013; Sherstneva et al. 2016b), the membrane potential was described based on the stationary solution of Eq. (1) because the generation of electrical responses in higher plants is a relatively slow process in most cases. Simplification accelerates the calculation in the analysis of complex models of electrical activity in plants.

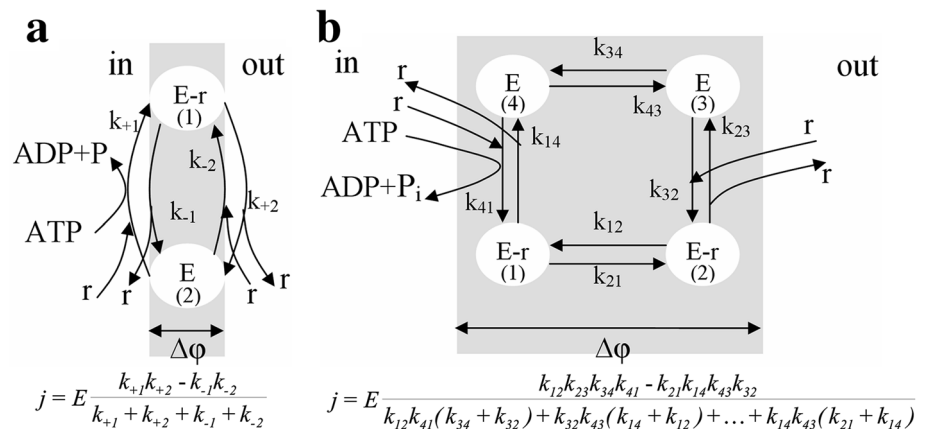
Electrogenic transporters include ion channels, the primary active transport system (mainly, ion-transporting ATPases) and the secondary active transport system (mainly, ion symporters and antiporters). The Goldman–Hodgkin–Katz flux equation is widely used to describe fluxes through ion channels and the secondary active transport system (Gradmann and Hoffstadt 1998a, b; Gradmann 2001a, b; Sukhov and Vodeneev 2009; Sukhov et al. 2011a, 2013; Hills et al. 2012; Beilby and Al Khazaaly 2016; Novikova et al. 2017) because it can describe the dependence of the flux on the membrane potential and ion concentrations. An alternative approach is based on the Hodgkin–Huxley model: electrical currents

(fluxes) are described on the basis of modified ohmic equations and are dependent on the membrane potential, ion equilibrium potentials and conductance of transporters (Beilby 1982; Mummert and Gradmann 1991; Gradmann et al. 1993). This approach describes the influence of the membrane potential on ion fluxes, but it does not consider the dependence of transporter conductance on ion concentrations. A parameterization of models of electrogenic transporters is often based on analysis of the current–voltage characteristics (Hills et al. 2012), which can be also used for the investigation of properties of ions transporters under different environmental conditions (Beilby and Casanova 2014; Beilby and Al Khazaaly 2016).

Ion-transporting ATPases can also be described on the basis of a modified ohmic equation (Mummert and Gradmann 1991; Gradmann et al. 1993; Gradmann and Hoffstadt 1998a, b; Gradmann 2001a, b); however, the equation cannot simulate the dependence of flux through the ATPase on ion concentrations. In particular, the effect of flux saturation cannot be described. Kinetic models describing two, four or more states of the enzyme (Hansen et al. 1981, 1983) are another tool for the simulation of ion-transporting ATPases. In ‘two-state’ models (Fig. 2a), ion transport includes two stages, each of which includes the bonding and decay of ions (Sukhov and Vodeneev 2009; Sukhov et al. 2013; Beilby and Al Khazaaly 2016). The first stage is connected to ATP hydrolysis and is not dependent on the membrane potential; the second stage is dependent on the membrane potential. The current–voltage characteristics can be used for the parameterization of the model (Hansen et al. 1981, 1983). Models of ion-transporting ATPases can also include more than two states. ‘Four-state’ models (Fig. 2b) separately describe the ATP-dependent bonding and decay of ions on the cytoplasmic side of the membrane, the bonding and decay on the opposite side, and translocations of the enzyme and the complex of enzyme and ion(s) through the membrane (Hills et al. 2012). The translocations can be potential dependent (charge transfer) or potential independent (transfer of neutral molecule). ‘Multi-state’ models describe ion-transporting ATPases in details (Fisahn et al. 1992); however, they are complicated and have far too many parameters. The equation of Läuger and Stark (1970) or the Goldman–Hodgkin–Katz flux equation (Sukhov and Vodeneev 2009) can be used to describe the dependence of ion transfer on the membrane potential in the different models of ion-transporting ATPases.

Simulation of the non-stationary electrical activity (LERs, ESs, oscillations) requires description of the regulatory mechanisms for ion transporters. This mechanism is a gating in different ion channels that participate in the generation of electrical responses in plants. There are two main approaches to the description of the gating in a plant ion channel. First, the gating can be described by a model of

Fig. 2 ‘Two-state’ (a) and ‘four-state’ (b) models of ion-transporting ATPases (Hansen et al. 1981; Sukhov and Vodeneev 2009): j is the flux of ions through ATPase; E is the concentration of the enzyme in the membrane; k_{+1} , k_{+2} , k_{+3} , and k_{+4} are rate constants for the forward transport of ion(s) by ATPase; k_{-1} , k_{-2} , k_{-3} , and k_{-4} are rate constants for the backward transport of ion(s) by ATPase



several independent gating particles that activate or inactivate the channel (Hodgkin and Huxley 1952). This model was used to simulate the dynamics of the activities of calcium and chloride ion channels in algae (Beilby 1982, 2007). However, the activation/inactivation of ions channels is instead connected with the translocation of charged segments of the channel and changes in its conformation (Fig. 3a) (Dreyer and Blatt 2009), i.e. being constructed of independent gating particles is unlikely. An alternative approach has been proposed in the works of Gradmann (Mummert and Gradmann 1991; Gradmann et al. 1993; Gradmann and Hoffstadt 1998a, b; Gradmann 2001a, b). This approach (Fig. 3b) considers closed and open states (inward and outward K^+ channels, Cl^- channels in some models) or closed, open and inactivated states (Ca^{2+} channels, Cl^- channels in some models) (Gradmann 2001a, b; Sukhov and Vodeneev 2009; Beilby and Al Khazaaly 2016). In this case, the probabilities of these states are variables in the model of electrical activity; the dependence of the probabilities on the membrane potential can be described based on the equations of Lauser and Stark (Lauser and Stark 1970; Gradmann 2001a, b). It should be noted that this approach can be also used to describe the potential-dependent regulation of transport ATPases (Mummert and Gradmann 1991; Gradmann 2001a, b).

The regulation of the activities of transporters by ligands is possible in models that consider changes in the concentrations of regulatory agents in cell compartments (e.g. the cytoplasm). In particular, inositol-3-phosphate (Wacke and Thiel 2001; Wacke et al. 2003; Beilby and Al Khazaaly 2016; Novikova et al. 2017), Ca^{2+} (Sukhov and Vodeneev 2009; Hills et al. 2012; Sukhov et al. 2012; Novikova et al. 2017) and H^+ (Hills et al. 2012) have been described as such agents in different models. The Hill equation is widely used to describe the regulation of the activities of ion transporters by different ligands in models of electrical activity in plants (Sukhov and Vodeneev 2009; Hills et al. 2012; Novikova et al. 2017) and can also be

used for the regulation of transporter activities by physical factors (e.g. light) (Hills et al. 2012). It should be noted that simulation of the regulation of certain transport processes (e.g. the regulation of Ca^{2+} channels affecting internal stores by inositol-3-phosphate) requires the description of several states of ion transporters and the solution of differential equations (Wacke and Thiel 2001; Wacke et al. 2003; Beilby and Al Khazaaly 2016).

In addition to descriptions of the membrane potential, ion transporters and their regulation, the models of electrical activity in plants can consider changes in the concentrations of ions and the buffer capacities of the apoplast, cytoplasm, vacuole, etc. (Gradmann 2001a, b; Shabala et al. 2006; Sukhov and Vodeneev 2009; Hills et al. 2012; Novikova et al. 2017). The buffer capacities can be described using the chemical equations of the interaction of the buffer and ions (Gradmann 2001a, b; Sukhov and Vodeneev 2009; Novikova et al. 2017) or based on empirical equations (Hills et al. 2012; Novikova et al. 2017). In addition, some models of electrical responses in plants (Sukhov and Vodeneev 2009; Vodeneev et al. 2012; Sukhov et al. 2013; Novikova et al. 2017) describe the reception of the action of environmental factors and/or the action of regulatory agents on plant cells (e.g. changes in temperature using Q_{10}).

Thus, there are a number of approaches to the detailed simulation of the electrical activity in plants. However, there are other ways to describe plant electrical responses. One approach is based on equivalent electrical circuits, which include only standard electrical elements (batteries, resistors, capacitors, diodes, switches, etc.) without an additional description of regulatory processes. The elements qualitatively reflect general properties of the biological membrane and the main groups of ion transporters in this membrane (Volkov et al. 2009, 2010, 2017). In some works, these equivalent electrical circuits were used for the theoretical prediction of the electrical properties of plants (Volkov et al. 2009, 2010) and to analyse the results of experimental measurements (Volkov et al. 2017).

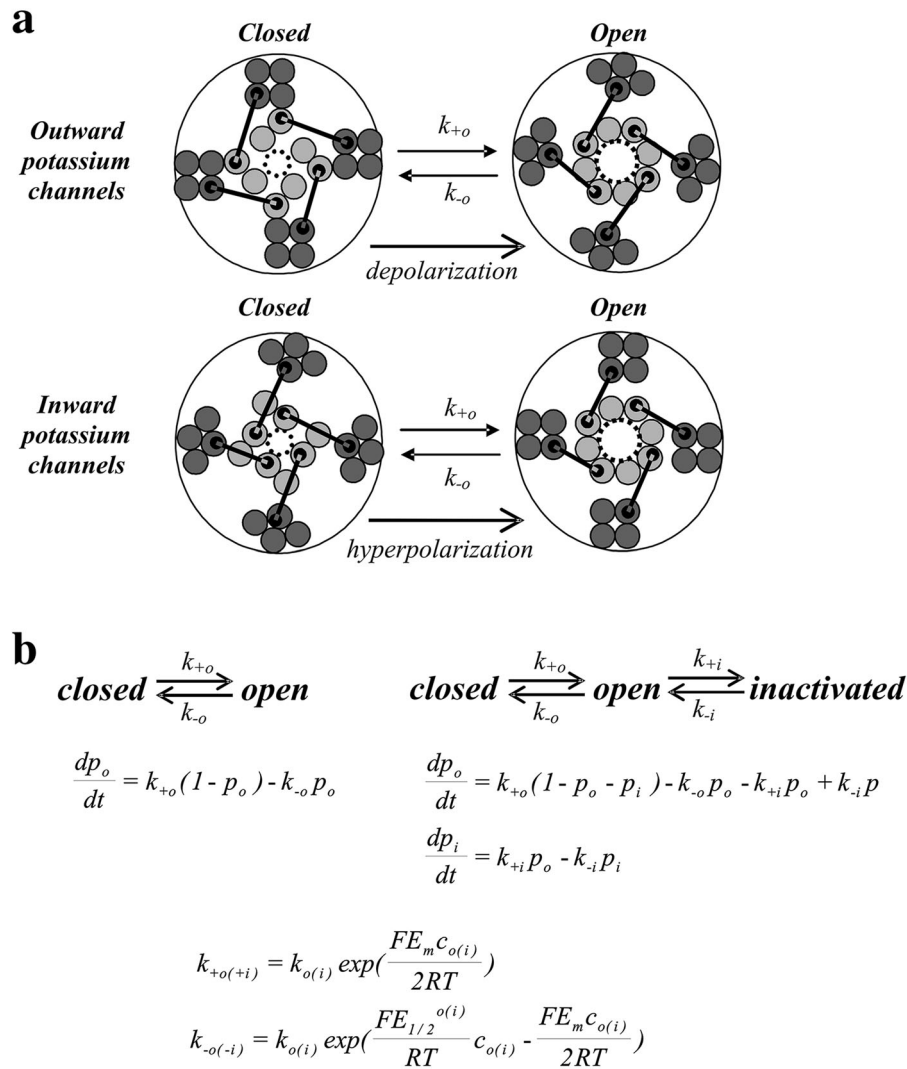


Fig. 3 A model of gating of the ion channel. **a** Schema of gating of potential-dependent potassium ion channels (Dreyer and Blatt 2009). The shift of voltage-sensing modules dislocates other segments of the channel such as the lens diaphragm, and the channel is opened or closed; k_{+o} and k_{-o} are rate constants of the opening and closing of the ion channel. **b** Kinetic model of activation of ion channel with two (left) or three (right) states (Gradmann and Hoffstadt 1998a, b; Sukhov and Vodenev 2009); p_o and p_i are the probabilities of open and closed states of the channel, respectively; k_{+i} and k_{-i} are the rate

constants of the transition from the opened state to inactivated states and back; E_m is the membrane potential. F , R and T are standard thermodynamic values. $E_{1/2}^{o(i)}$ is the energy difference between open and closed states (open and inactivated ones); $c_{o(i)}$ is a constant, for the transition from closed to open states (open to inactivated ones), which represents a portion of the membrane potential acting on the gating mechanism and charge of this mechanism; and $k_{o(i)}$ is the rate constant of transition between closed and open states (open and inactivated ones) at E_m and $E_{1/2}^{o(i)}$ equal to zero

Another approach is based on the application of regression equations that connect parameters the stimulation ('input') and parameters of the electrical response ('output'); both linear and nonlinear systems of estimators can be used (Chatterjee et al. 2014, 2015). Neural networks can also be used to describe the connections between 'input' and 'output' (Chen et al. 2016). The main advantage of this approach is the possibility of predicting the electrical activity under a given stimulation (or detecting stimulation parameters based on the properties of electrical responses) without information about the mechanisms of generation of the electrical responses.

However, these models cannot be used to investigate the mechanisms of electrical responses and cannot predict the responses of the plant cell to novel, unknown conditions.

Basic Mathematical Models of Generation of Electrical Responses in Plants

The first mathematical model of the generation of electrical responses in plants was proposed in the works of (Beilby and Coster 1979; Beilby 1981, 1982), which adapted the

Hodgkin–Huxley model to describe the action potential in *Chara* (Fig. 4a). The model included the activities of Ca^{2+} and Cl^- channels and a reductive description of the dynamics of gating particles in these channels (gating particles relax to new stationary states); the activity of Na^+ channels was not described in the model, because the channels seems to be unique to animal kingdom and that part of the Hodgkin–Huxley model is unsuitable for plants. The model of Beilby described the experimental AP in *Chara* well and showed that the Hodgkin–Huxley model can be used to simulate plant electrical activity. However, a number of fundamental properties of plant electrogenesis (the active transport of ions, changes in ion concentrations and buffer capacities, the regulation of transporters by ligands, etc.) were not considered in the model.

Despite these restrictions, the Hodgkin–Huxley model was used in some models of ESs in higher plants. In particular, the model of Zhao et al. (2013) described a multicellular system in which each cell is a point source of electrical current, and this current was simulated based on the modified Hodgkin–Huxley equation. The Laplace equation described changes in the electrical potential in extracellular space. The model was used to investigate the quantitative relationship between the intracellular and extracellular potentials of plant cells. It was shown that the results of extracellular measurements were a spatiotemporal superposition of signals induced by the simultaneous electrical activities of numerous cells in plants.

The next model of plant electrical activity simulated AP in the green algae *Acetabularia* (Mummert and Gradmann 1991). This model described a system of passive and active ion transporters (Cl^- -ATPase, K^+ and Cl^- channels) and their regulation by membrane potential, based on a calculation of the probability of the open state of the transporter. The model quantitatively described the depolarization-induced AP in *Acetabularia*. However, it was not used to analyse the electrical activity of higher plants, liverworts, and *Characeae*, because the mechanism of AP generation in *Acetabularia* (a transient inactivation of Cl^- -ATPase) is unique (Gradmann 1976).

The later models of Gradmann and co-workers (Gradmann et al. 1993; Gradmann and Buschmann 1997; Gradmann and Hoffstadt 1998a, b; Gradmann 2001a, b) described electrical oscillations in higher plants (Fig. 4b). All models were based on the kinetic description of regulation of systems of ions transport, including active transporters of ions (Gradmann and Boyd 2005) and ion channels (Gradmann et al. 1993; Gradmann and Buschmann 1997). The description took into account two or three states of transporters, the states had different activities, and the transitions between states were dependent on the membrane potential. All models described Cl^- , inward and outward K^+ channels, H^+ -ATPase and $2\text{H}^+/\text{Cl}^-$

symporter. The descriptions of transporters were based on the modified ohmic equations in early models (Gradmann et al. 1993) and on the Goldman–Hodgkin–Katz flux equation in the later models (Gradmann and Hoffstadt 1998a, b; Gradmann 2001a, b). Changes in ion concentrations in the cytoplasm and apoplast and their buffer capacities were also described in the models (Gradmann 2001a, b).

Analysis of Gradmann’s models (Gradmann et al. 1993; Gradmann and Hoffstadt 1998a, b; Gradmann 2001a, b) of the electrical activity in plants showed that the models described a periodic generation of electrical impulses, and the dynamics of the membrane potential during these oscillations was similar to the dynamics during the generation of AP in plants. The parameters of the oscillations were dependent on apoplast volume (Gradmann 2001a) and ion concentrations (Gradmann and Hoffstadt 1998a, b). In addition, it has been shown (Shabala et al. 2006) that Gradmann’s model of electrical oscillations imitated periodic changes in ions fluxes. These periodic changes were observed in certain ranges of external temperatures and ionic concentrations; the activity of H^+ -ATPase and cell size also influenced the parameters of the simulated oscillations (Shabala et al. 2006).

The models of electrical oscillations by Gradmann and co-workers (Gradmann et al. 1993; Gradmann and Hoffstadt 1998a, b; Gradmann 2001a, b) simulated periodic electrical responses in plants well; however, there were several problems that required subsequent works. (i) Gradmann’s models were not used for the simulation of stimulus-induced electrical responses (LERs and ESs). (ii) These models did not consider certain non-electrogenic systems of ion transport (e.g. H^+/K^+ -antiporter), and the absence of these transporters can influence the simulated stationary ion concentrations. (iii) The models did not describe the regulation of ion transporters by Ca^{2+} and other chemical ligands. As a result, other models of the plant’s electrical activity were developed.

The problems were partly solved in our models of electrical responses in plants (Sukhov and Vodeneev 2009; Sukhov et al. 2013; Sherstneva et al. 2016b). The first was the model of the generation of action potential in higher plants (Sukhov and Vodeneev 2009). This model was based on Gradmann’s detailed description of electrical activity in plants (Gradmann 2001a, b); however, it had a number of new elements. First, the model described the regulation of H^+ -ATPase and Cl^- channel activities by Ca^{2+} ; Ca^{2+} channels and Ca^{2+} -ATPase were included in the model (Sukhov and Vodeneev 2009). Second, the model described the K^+/H^+ -antiporter, which participated in establishing the stationary K^+ and H^+ concentrations. The proposed model imitated electrical- and cooling-induced LERs, which included APs, were similar to

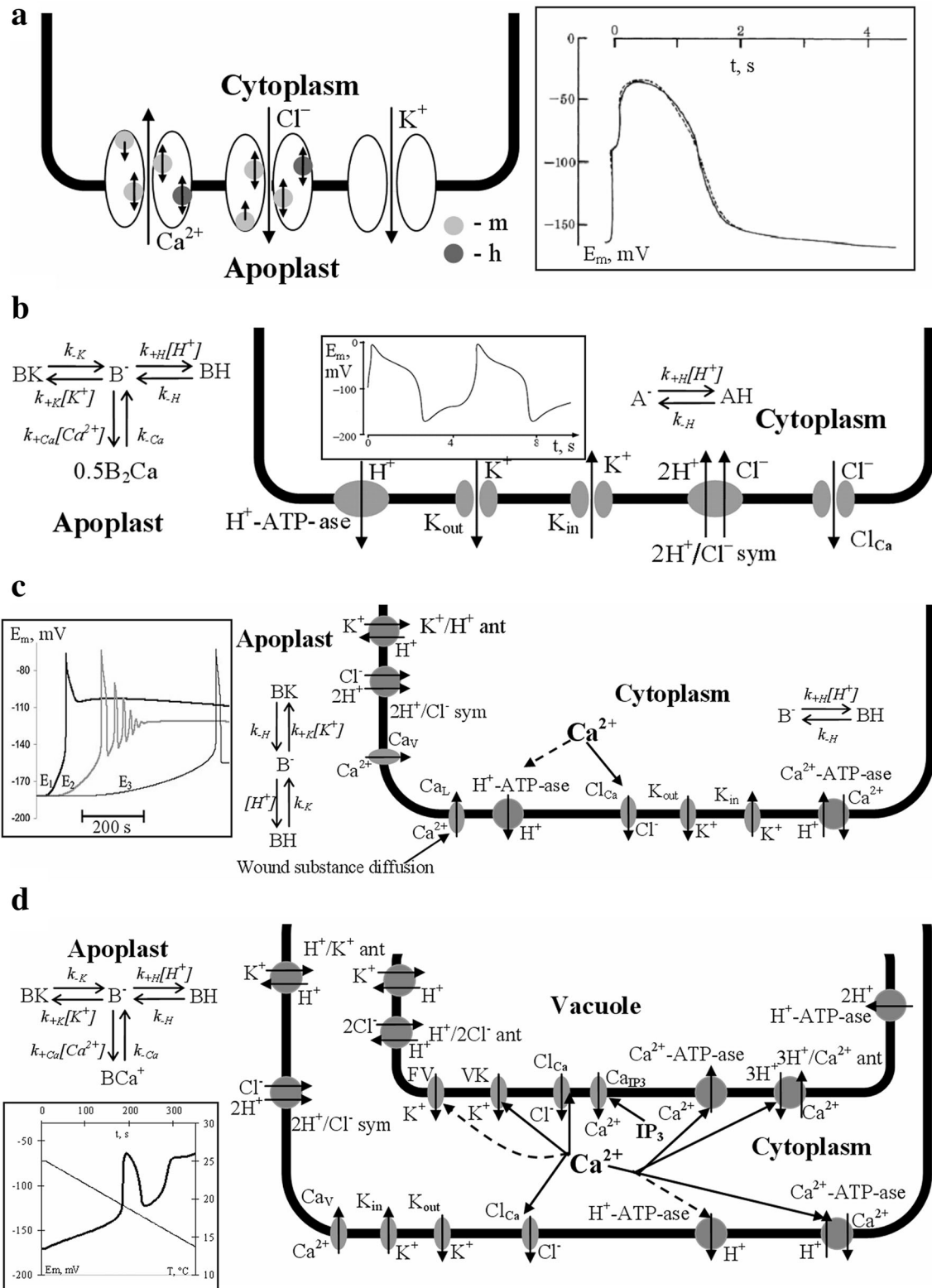


Fig. 4 Schemes of some models of the generation of electrical responses and examples of these responses (inserts in *rectangular boxes*). **a** Model of generation of the action potential using the modified Hodgkin–Huxley model (based on Beilby 1982). **b** Model of electrical oscillations in plants (based on Gradmann 2001b). **c** Model of generation of the variation potential (based on Sukhov et al. 2013). **d** Model of generation of the action potential including the vacuole (based on Novikova et al. 2017). E_m is the membrane potential; m and h are activation and inactivation gating particles; Ca_L , Ca_V , K_{in} and K_{out} are ligand- and potential-dependent calcium channels and inward and outward potassium channels in the plasma membrane; Ca_{IP_3} , FV and VK are inositol-3-phosphate-dependent calcium channels, Ca^{2+} -inactivated and Ca^{2+} -activated potassium channels in the tonoplast; Cl_{Ca} is Ca^{2+} -activated chloride channels in the plasma membrane and tonoplast; H^+ - and Ca^{2+} -ATP-ases are transport ATP-ases of the plasma membrane and tonoplast; $H^+/2Cl^-$ ant and $3H^+/Ca^{2+}$ ant are $H^+/2Cl^-$ - and $3H^+/Ca^{2+}$ -antiporters in the tonoplast; $2H^+/Cl^-$ sym is the $2H^+/Cl^-$ -symporter in the plasma membrane; H^+/K^+ ant is the neutral H^+/K^+ -antiporter in the plasma membrane and tonoplast; B^- , BH , BK , BCa^+ and B_2Ca are free, H^+ , K^+ and Ca^{2+} bound buffer molecules in the apoplast; k_{+H} , k_{+K} , k_{+Ca} and k_{-H} , k_{-K} , k_{-Ca} are rate constant association and dissociation of buffer with protons, potassium and calcium ions; and IP_3 is inositol-3-phosphate. *Solid* and *dotted arrows* from Ca^{2+} , IP_3 and wound substance show the positive and negative regulation of ion transporters by the agents

experimental electrical responses and were suppressed at a low concentration of external Ca^{2+} (Sukhov and Vodeneev 2009). Analysis of the model theoretically showed that H^+ -ATPase played the main role in the resting electrical potential of the plasma membrane and in the repolarization during AP. This result is in a good accordance with the literature data about the important role of the H^+ -ATPase in the formation of the resting membrane potential in *Characeae* (Beilby 1984) and guard cells of higher plants (Blatt 1987). It has also been shown that the Ca^{2+} -dependent transient inactivation of the H^+ -ATPase weakly participated in the development of the AP depolarization; however, it played the key role in the development of pH changes during the generation of the action potential (Sukhov and Vodeneev 2009).

The work of Sukhov and Vodeneev (2009) was based on modelling the variation potential (Sukhov et al. 2013) (Fig. 4c). The VP model additionally described the production and propagation of the specific chemical signal (wound substance, WS) that was likely to participate in the propagation of the variation potential (Vodeneev et al. 2012, 2015) and the subsequent activation of the WS-dependent Ca^{2+} channels, which caused the development of the electrical response (Sukhov et al. 2013). The simulation showed that the parameters of VP (amplitude, number of ‘AP-like’ spikes, shape, etc.) were dependent on the amount of WS (i.e. the intensity of damage) (Sukhov et al. 2013). Later, this VP model was used for the theoretical analysis of the influence of the variation potential on photosynthetic parameters (Sherstneva et al. 2016b). Based on previous experimental results (Sherstneva et al. 2016a),

empirical linear dependences of the photosynthetic parameters on changes in intra- and extracellular pH were used. It was shown (Sherstneva et al. 2016b) that the VP model simulated the dependence of the photosynthetic response on the intensity of damage and distance from the damaged zone.

It should be noted that the described models of electrical activity in plants did not take into account the participation of intracellular compartments (endoplasmic reticulum, vacuole, chloroplast, mitochondria, etc.) in the generation of electrical responses and/or the development of physiological changes. The mathematical models of the next group considered the transmission of signals from the plasma membrane and cytoplasm to intracellular compartments. The imitation of this transmission can be used for detailed descriptions of the generation of electrical response as well as for simulation of the development of changes in physiological processes.

A number of models in this group simulated the participation of intracellular sources of Ca^{2+} in the generation of electrical responses. The model of Biskup et al. (1999), which simulated excitation in *Chara*, considered an intracellular source of Ca^{2+} and described the additional increase in the concentration of calcium ions during the generation of the electrical response. Later, other investigators (Wacke and Thiel 2001; Wacke et al. 2003) adapted Othmer’s model (Othmer 1997) to describe the AP generation in *Chara*. The model of (Wacke and Thiel 2001; Wacke et al. 2003) included IP_3 -dependent Ca^{2+} channels in intracellular compartments, which were also Ca^{2+} dependent, and described the processes of synthesis and utilization of inositol-3-phosphate. This model simulated an electrical current-induced transient increase in Ca^{2+} concentration (Ca^{2+} spikes) and showed the participation of the endoplasmic reticulum in the excitation of *Chara* (Wacke and Thiel 2001; Wacke et al. 2003); however, the dynamics of the membrane potentials were absent in these works.

The Wacke and Thiel model has been used in some later models that simulated the action potential in plants. A model by Beilby and Al Khazaaly (2016) simulated the action potential in *Chara*. This model described IP_3 and Ca^{2+} dynamics using the Wacke and Thiel model; the Ca^{2+} influx through TRP (transient receptor potential)-like channels was also assumed in the model. Ion transporters were described using modified ohmic equations, the Goldman–Hodgkin–Katz flux equations and ‘two-state’ models of transporting ATPase. Analysis of the model showed that it simulated experimental APs in *Chara* under controlled conditions and at high concentrations of NaCl (Beilby and Al Khazaaly 2016). The Wacke and Thiel model was also used in our previous model of AP in the cells of higher plants (Novikova et al. 2017) to describe the

dynamics of the concentration of IP_3 , which activated Ca^{2+} channels in the tonoplast (Fig. 4d). The model also described the K^+ and Cl^- channels of the vacuolar membranes. Descriptions of other transport and regulatory processes were based on the model of Sukhov and Vodennev (2009) with modifications. Analysis of the model showed (Novikova et al. 2017) that growths of the volume and area of the vacuole increased the threshold for AP generation; however, the activation of calcium channels in the tonoplast was able to participate weakly in the generation of action potential in higher plants.

The next model addressed the activity of stomatal guard cells (Hills et al. 2012, computational platform ‘OnGuard’) and also described the generation of electrical responses in signals to intracellular compartments (vacuole) and the development of the physiological response (opening/closing stomata). This model described numerous ion transporters in the plasma membrane and tonoplast, buffers, different regulatory processes (including the regulation of ion transport by Ca^{2+} , H^+ and light), the metabolism of sucrose and malate, etc. It should be separately noted that this model described the pressure in compartments of the cell and its influence on stomatal aperture. This model by Hills et al. (2012) was in good accordance with experimental results and was used for the theoretical analysis of stomatal activities under different conditions, including electrical activities. Chen et al. (2012) used the model ‘OnGuard’ to investigate ion fluxes during the diurnal cycle; Minguet-Parramona et al. (2016) studied the participation of ion-transporting systems in the generation of Ca^{2+} oscillations and the role of these oscillations in the closing of stomatal guard cells. It should be noted that theoretical analysis in the previous work showed the mechanism of periodic opening of stomata, which was based on the interaction between active and passive ion transporters, oscillations of the membrane potential and changes in ion concentrations. Thus, the model by Hills et al. (2012) is the unique example of a model of electrical activity that describes electrical responses, signals to intracellular compartments and the development of the physiological response. However, this model describes only one (very important) physiological process, and the simulation of other electrical response-induced physiological changes (changes in photosynthesis, respiration, transpiration, resistance to stressors, etc.) is an important future task.

A review of ‘mechanistic’ models of the generation of electrical responses shows the following tendency: early models describe ion transporters in the plasma membrane, whereas contemporary models simulate signal transduction to intracellular compartments and the development of physiological changes. It is possible that future perspectives on the detailed simulation of electrical responses will

be connected to the elaboration of models of the physiological responses of the plant cell to stressors, which will be based on descriptions of the electrical activity. These models (similar to ‘OnGuard’ by Hills et al. 2012) can be used to predict the response of plant cells under various environmental conditions.

However, the solution to the problem of predicting plant responses can be based on other approaches. First, regression equations (or neural networks) that connect the stimulation parameters (‘input’) and electrical response parameters (‘output’). This approach was used in the work of Chatterjee et al. (2014), which tested the efficiency of various linear (ARX, ARMAX, BJ and OE) and nonlinear (Nonlinear Hammerstein–Wiener and NLARX) estimators for the forward modelling of the electrical response induced by light in plant leaves, and the inverse modelling of the parameters of light stimuli based on experimental electrical responses. In the next work by Chatterjee et al. (2015), this approach was used to identify different stimuli (sodium chloride, sulphuric acid and ozone), based on the parameters of experimental electrical responses. An interesting example of inverse modelling was the work of Aditya et al. (2011), which used the inverse fast Fourier transform of parameters of the light-induced electrical activity in plants for control of the biomachine. The work of Chen et al. (2016), which used neural networks for classification of ESs, should also be noted. Thus, ‘non-mechanistic’ models are also being developed; it is possible that in future work, the models will be used for monitoring environmental conditions and plant physiological states.

Another approach is based on equivalent electrical circuits composed of standard electrical elements that imitate the electrical properties of plants. These circuits were developed for Venus flytrap (*Dionaea muscipula*) (Volkov et al. 2009), sensitive plant (*Mimosa pudica*) (Volkov et al. 2010, 2014), and aloe (*Aloe vera* L.) (Volkov et al. 2017).

Mathematical Models of Propagation of Electrical Signals in Plants

Simulating the propagation of long-distance signals through the plant is another important direction of modelling electrical activity. Simulation is an effective tool for the theoretical investigation of the connection between local electrical responses in the stimulated zone and physiological changes in unstimulated parts of the plant. There are various approaches to the description of ES propagation: a solitonic model (Maška and Pietruszka 1995; Pietruszka et al. 1997), systems of electrically coupled excitable elements (Garkusha et al. 2002; Sukhov et al. 2011a, b), equivalent electrical circuits (Volkov et al. 2017), the transmission of ‘wound substance’ by a mass

flow (Malone 1994) or turbulent diffusion (Vodeneev et al. 2012; Sukhov et al. 2013).

The model of AP propagation in plants by Pietruszka et al. (1997) was based on the similarity between the propagation of AP and the transmission of solitons (Maška and Pietruszka 1995; Pietruszka et al. 1997). According to the Frenkel–Kontorova–Tomlinson model (Weiss and Elmer 1997), the transmission of soliton in a one-dimensional mechanical system can be described as the transduction of motion from the moving particle to the immobile one. This transmission is similar to AP propagation in the live organism: excited (depolarized) parts of the plasma membrane correspond to moving particles, while unexcited parts correspond to immobile particles. The model of AP propagation in plants (Pietruszka et al. 1997) described the electrical fields of K^+ , Ca^{2+} and Cl^- using the full Lagrangian density function. The numerical solutions of the model's equations included solutions (travelling waves) that preserve the shape and move without dissipation. The solutions were interpreted as propagating AP in plants. However, the model of Pietruszka et al. (1997) was not based on a detailed description of mechanisms of AP generation and propagation; therefore, its application to the analysis of the AP propagation is very limited.

The propagation of electrical signals can also be described by equivalent electrical circuits (Tsaplev and Zatsepina 1980; Opritov et al. 1991; Vodeneev et al. 2016; Volkov et al. 2017). First, the equivalent electrical circuits can be used to describe the passive propagation of electrotonic potentials in higher plants (Volkov et al. 2017). Second, the active propagation of ESs can be described based on the cable equation (Tsaplev and Zatsepina 1980; Opritov et al. 1991; Beilby 2007; Vodeneev et al. 2016). In this case, the ES-conducting excitable medium is simplistically described as a one-dimensional long cell or a chain of electrically coupled excitable cells (as in Chara algae, Sibaoka and Tabata 1981). The models imitated some properties of ESs, including the constant velocity of propagation (Tsaplev and Zatsepina 1980; Opritov et al. 1991; Beilby 2007). However, the ESs propagation is likely to be connected with three-dimensional excitable medium in higher plants, e.g. the symplast of parenchyma cells (Opritov et al. 1991; Vodeneev et al. 2016) or the symplast of parenchyma cells and sieve elements (Fromm and Lautner 2007).

The analysis of ES propagation in two-dimensional systems of excitable cells is another approach to the investigation of the transmission of electrical signals in plants. In the simplest variant, the analysis can be based on cellular automation models (Gerhardt et al. 1990). Garkusha et al. (2002) used the cellular automation model to describe the propagation of the light-induced ES

(Fig. 5a). A two-dimensional system of cells was used, the electrical current during generation of ES in each cell was described as two meanders, and the probabilities of activation of neighbouring cells were used to describe the transmission of the electrical signal. This model (Garkusha et al. 2002) shows the effect of ES-simulated dependence of the signal's velocity on the duration of depolarization and the probabilities of activation of neighbouring cells.

Models of the next group (Sukhov et al. 2011a, b) use the detailed description of the generation of the electrical response. Both models were based on the two-dimensional system of excitable elements (cells) with local electrical connections (Fig. 5b). The first model (Sukhov et al. 2011a) used previous descriptions of AP generation (Sukhov and Vodeneev 2009), which took into account ions transporters, Ca^{2+} regulation, cytoplasmic and apoplastic buffers, etc.; the ion fluxes between apoplasts of neighbouring cells were also described. Analysis of the model of AP propagation showed that it imitated the passive (electrotonic) and active propagation of the action potential; the parameters of this propagation were similar to the experimental values (Sukhov et al. 2011a). The model also showed that increasing the electrical conductance between cells accelerated the propagation of AP; however, this increase raised the threshold for generation of action potential. It should be noted that the model (Sukhov et al. 2011a) described a system of homogeneous elements, i.e. a symplast of excitable parenchyma in the vascular bundles, but sieve elements are the possible way of the action potential propagation, too (Fromm and Lautner 2007). Another model (Sukhov et al. 2011b) described the AP propagation through the heterogeneous system of elements: the two-dimensional system of high-excitability cells (symplast) included lines of cells with the high intercellular conductance and low excitability (sieve elements). The FitzHugh–Nagumo model was used to describe AP generation in each of the cells. Analysis of this heterogeneous model showed that a combination of the symplast of parenchyma cells and sieve elements contributed to more effective generation and propagation of electrical signals than the homogeneous system, including high-excitability elements with low intercellular electrical conductance or low-excitability elements with high intercellular electrical conductance (Sukhov et al. 2011b).

Thus, the application of two-dimensional systems of excitable elements (in future work, three-dimensional ones) is an effective tool for analysis of the propagation of the action potential in plants. However, the propagation of other important ESs in plants, namely, VP, can be connected to the transmission of hydraulic and/or chemical signals (Vodeneev et al. 2016); as a result, other methods of description of the signal propagation are necessary.

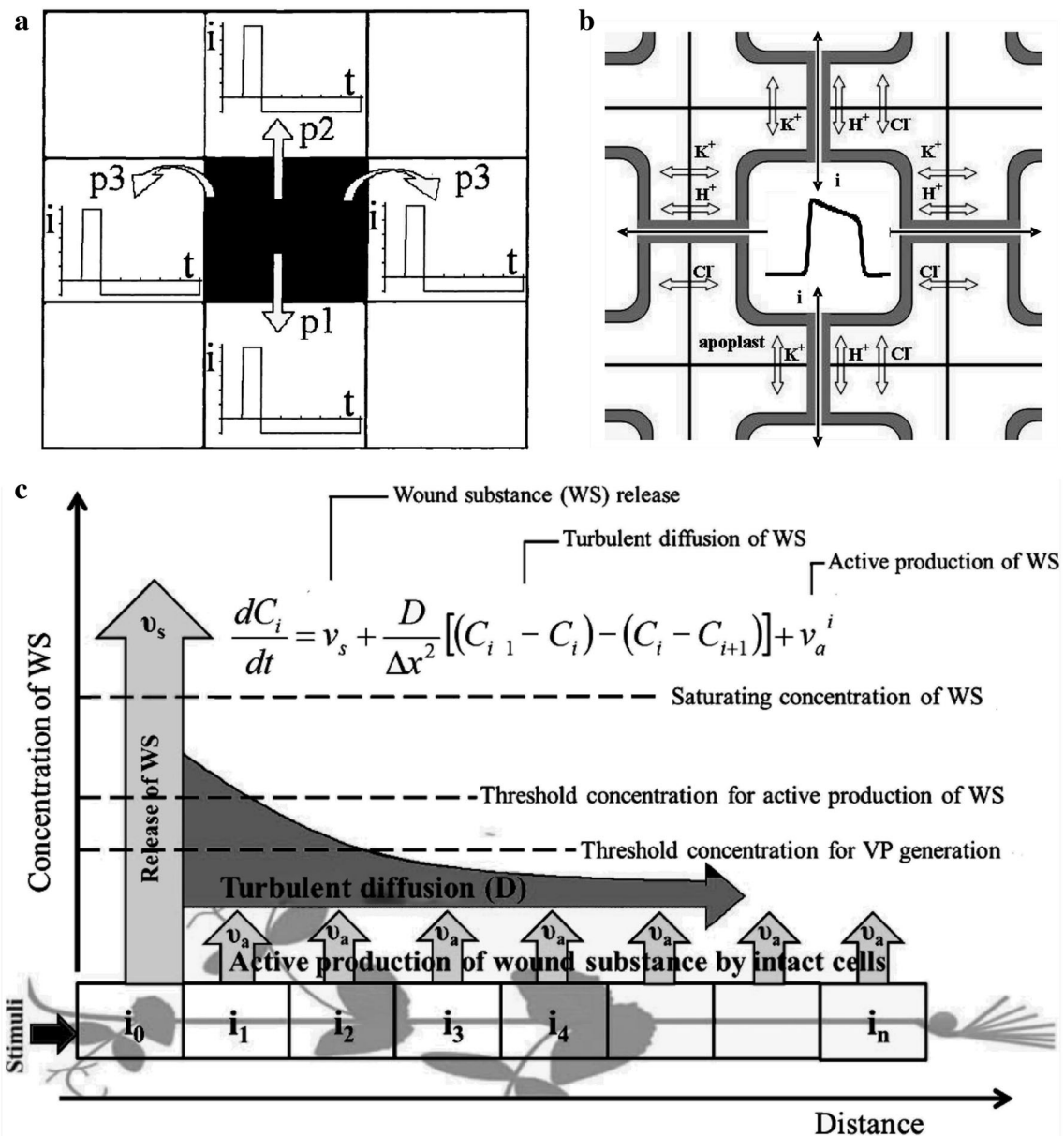


Fig. 5 Schemes of some models of propagation of electrical signals. **a** Model of electrical signal propagation based on the two-dimensional system of excitable elements based on the cellular automation (Garkusha et al. 2002, with modifications). **b** Model of action potential propagation through symplast of parenchyma cells in higher

plants (Sukhov et al. 2011a, b, with modifications). **c** Model of propagation of the variation potential based on turbulent diffusion and the secondary production of the wound substance (Vodeneev et al., 2017 with modifications). Here, $p1$, $p2$ and $p3$ are the probabilities of excitation of neighbouring elements

There are only a few models of VP propagation (Malone 1994; Vodeneev et al. 2012, 2015, 2017; Sukhov et al. 2013) based on the description of a chemical signal (transmission of wound substance, WS). First, Malone (1994) proposed the model of wound-induced mass flow, which induced the propagation of WS. This model was based on the Hagen–Poiseuille law. It was theoretically shown that the velocity of WS transmission can be on the order of tens of cm s^{-1} , and this mechanism can participate in VP propagation (Malone 1994; Vodeneev et al. 2015).

Second, our early works (Vodeneev et al. 2012; Sukhov et al. 2013) showed that WS transmission can be described by the one-dimensional diffusion equation. This description was correct for the diffusion of WS in turbulent flow (Vodeneev et al. 2012), which can be the result of water flow through xylem (Roth 1996) and changes in a hydraulic pressure after local damages (Vodeneev et al., 2012). The elaborated model imitated changes in VP parameters with the increasing distance from the damaged zone (Sukhov et al. 2013). This model was modified in a subsequent work

(Vodeneev et al. 2017); a new variant of the model additionally included the secondary production of WS in the undamaged parts of the plant (Fig. 5c). The modified model accurately described the dependence of the velocity of VP propagation on the type of damage (mechanical wounding, heat, and burn).

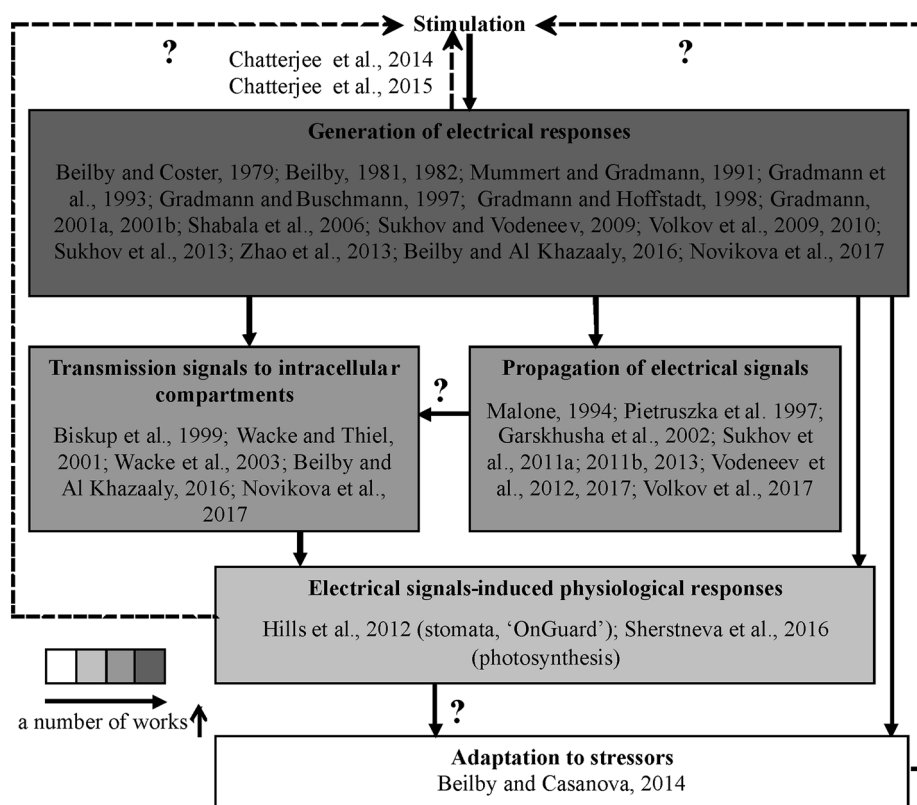
Conclusion and Future Perspective

A review of current works on the simulation of plant electrical activity (Fig. 6) shows that there are numerous models simulating the generation of electrical responses on the plasma membrane. Various descriptions are used in these models, from modifications of the classical Hodgkin–Huxley model to detailed models, including numerous ions transporters, regulatory processes, buffers, etc. These models are widely used in theoretical investigations of the mechanisms of electrical responses. A moderate number of works has simulated the processes of ES propagation. Simulation of the AP propagation and the electrotonic transmission of electrical signals are usually based on the equivalent electrical circuit or the system of electrically connected excitable elements. There are few models of VP propagation; they are based on descriptions of the propagation of chemical signals. The transmission of signals to intracellular compartments (endoplasmic reticulum,

vacuole) is also described in a moderate quantity of works. There are only a few works that describe the connection of the electrical activity and physiological processes; in particular, the ES influence on the functional state is weakly investigated. There are no models simulating the influence of electrical responses on the resistance of these organisms to adverse factors; however, there are a few works (Beilby and Casanova 2014; Beilby and Al Khazaaly 2016) which investigate the mechanisms of the salt tolerance of the *Chara* algae analysing the mathematical model of its electrical activity. The problem of inverse modelling (the identification of stimuli based on electrical response analysis) is also weakly investigated. In addition, it should be noted that the described models solve particular problems of plant electrogenesis, and the integration of these models into general models is a separate task.

Thus, the first problem of simulating plant electrical activity is the elaboration and development of models that simulate AP and VP propagations, the transmission of signals to intracellular compartments, the influence of ES on physiological processes and, especially, plant resistance to stressors. In particular, an interesting and important task is the elaboration of a model that simulates the reception of various external stressors by means of changes in electrical activity and imitates the development of physiological responses (modifications of photosynthesis, respiration, transpiration, resistance, etc.) to these stressors. With such

Fig. 6 Current status of simulation of different stages of development of electrical responses and ensuing physiological changes in plants



elaboration, the model will be an effective tool for the theoretical prediction of plant responses to various factors.

The second important problem of simulation of electrical activity in plants is the analysis of interaction of ESs propagation with the Ca^{2+} and ROS signals (Gilroy et al. 2016). It is probable that solution of the problem requires a description of activation of TPC channels and ROS cascades in the model, because this activation has recently been shown in plants (Hedrich et al. 2016).

The third general problem is the elaboration of a tool to integrate several specific models of different aspects of the plant electrical activity (specific models of the generation of electrical responses, their propagation, the transmission of signals to intracellular compartments, the development of various physiological responses, etc.) into the common model for the solution of the specific problem; different combinations of specific models can be used for solution of different specific problems in field of the plant electrogenesis. The tool will be a ‘*comprehensive model space*’ (this term was proposed for photosynthetic models, Nedbal et al. 2009), which will include a database of specific models of the electrical activity. The comprehensive model space will be used to choose a group of specific models for the analysis of the investigated problem, to hierarchically organize these models and to support the data communication between them.

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