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REVIEW

Electrical signals as mechanism of photosynthesis regulation in plants

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Abstract This review summarizes current works concerning the effects of electrical signals (ESs) on photosynthesis, the mechanisms of the effects, and its physiological role in plants. Local irritations of plants induce various photosynthetic responses in intact leaves, including fast and long-term inactivation of photosynthesis, and its activation. Irritation-induced ESs, including action potential, variation potential, and system potential, probably causes the photosynthetic responses in intact leaves. Probable mechanisms of induction of fast inactivation of photosynthesis are associated with Ca^{2+}- and (or) H^+-influxes during ESs generation; long-term inactivation of photosynthesis might be caused by Ca^{2+}- and (or) H^+-influxes, production of abscisic and jasmonic acids, and inactivation of phloem H^+-sucrose symporters. It is probable that subsequent development of inactivation of photosynthesis is mainly associated with decreased CO_2 influx and inactivation of the photosynthetic dark reactions, which induces decreased photochemical quantum yields of photosystems I and II and increased non-photochemical quenching of photosystem II fluorescence and cyclic electron flow around photosystem I. However, other pathways of the ESs influence on the photosynthetic light reactions are also possible. One of them might be associated with ES-connected acidification of chloroplast stroma inducing ferredoxin-NADP$^+$ reductase accumulation at the thylakoids in Tic62 and TROL complexes. Mechanisms of ES-induced activation of photosynthesis require further investigation. The probable ultimate effect of ES-induced photosynthetic responses in plant life is the increased photosynthetic machinery resistance to stressors, including high and low temperatures, and enhanced whole-plant resistance to environmental factors at least during 1 h after irritation.

Keywords Action potential · Electrical signals · Photosynthesis · Photosynthesis regulation · System potential · Variation potential

Introduction

Photosynthesis is the transformation of light energy into chemical energy, and it is the basis of the life of green plants. Regulation of photosynthesis under different environmental conditions is a fundamental activity for plants. There are numerous mechanisms of photosynthesis regulation including state transition (Murata 2009; Tikkanen and Aro 2014), non-photochemical quenching (NPQ) of photosystem II (PSII) fluorescence (Müller et al. 2001; Bukhov 2004), ferredoxin-NADP$^+$ reductase accumulation at the thylakoids in Tic62 and TROL complexes (Alte et al. 2010; Benz et al. 2010), activation/inactivation of H^+-ATPsynthase (Evron et al. 2000), modification of cyclic electron flow around photosystem I (PSI) (Shikanai 2014), changes in the activities of Calvin–Benson cycle enzymes (Bukhov 2004), and many others. Systems of photosynthetic regulation are affected, for example, by light intensity (Bukhov 2004; Murata 2009; Tikkanen and Aro 2014), temperature (Pastenes and Horton 1996; Luo et al. 2011), and CO_2 concentration (Golding and Johnson 2003; Miyake et al. 2005).

Regulation of photosynthesis is especially important under stress conditions, e.g., very intense light, high and

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low temperatures, and drought. In these cases, various regulatory systems protect photosynthetic machinery (Munekage et al. 2004; Zhang and Sharkey 2009; Yamori et al. 2011; Huang et al. 2012; Zivcak et al. 2013). These systems can stimulate the repair processes of the photosynthetic machinery after stress, too (Allakhverdiev et al. 2005, 2008; Nath et al. 2013). Stress-induced photosynthetic changes may participate in defense responses on a whole-cell level (Pfannschmidt et al. 2001).

The local action of stressors (e.g., high temperature, mechanical wounding, shifts in water regime, and electric current) can change photosynthetic processes in intact parts of the plant (Herde et al. 1995, 1999a; Peña-Cortés et al. 1995; Fromm and Fei 1998; Koziolek et al. 2004; Hlaváčková et al. 2006; Krupenina and Bulychev 2007; Grams et al. 2007, 2009; Pavlovič et al. 2011; Hlavinka et al. 2012; Sukhov et al. 2012, 2013b, 2014a, b; Fromm et al. 2013; Bulychev and Komarova 2014). Fast (Krupenina and Bulychev 2007; Grams et al. 2009; Pavlovič et al. 2011; Sukhov et al. 2012, 2014a) and long-term (Herde et al. 1999a; Hlaváčková et al. 2006; Fromm et al. 2013) inactivation of photosynthesis, and its activation (Fromm and Fei 1998; Grams et al. 2007) have been observed after local irritations in different combinations of photosynthetic responses. The results show that there are signals that connect the irritated zone with the intact parts of the plant.

These signals can be hormonal, hydraulic, and electrical; moreover, different signals may interact (Fromm and Lautner 2007; Gallé et al. 2015; Vodeneev et al. 2015). Electrical signals (ESs) play key roles in the induction of photosynthetic responses over the minutes to tens of minutes range (Lautner et al. 2005; Grams et al. 2009; Sukhov et al. 2012, 2014b; Sherstneva et al. 2015). Analysis of the participation of ESs in the regulation of photosynthesis is the aim of the present review.

Electrical signals in plants

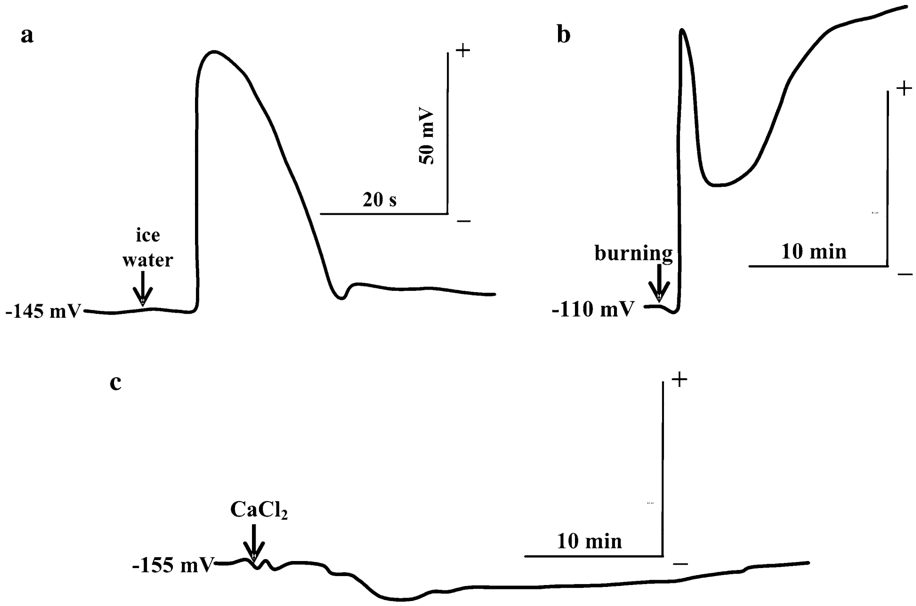
Various local irritations (e.g., high temperature, cooling, crush, prick, and touch) can induce the generation and propagation of ESs in plants (Fromm and Lautner 2007; Gallé et al. 2015; Vodeneev et al. 2015). Three plant's ESs are known (Vodeneev et al. 2015): the action potential (AP), variation potential (VP), and system potential (SP).

Plant's AP (Fig. 1a) is a short-term electrical reaction (seconds to tens of seconds), which included fast depolarization (decrease of an electric potential difference) and repolarization (recovery of the potential difference) of plasma membrane (Davies and Stankovic 2006; Trebacz et al. 2006; Beilby 2007). Additionally changes in the electric potential difference on tonoplast membrane can also participate in AP generation in algae (Beilby 2007). AP generation has all-or-none character, i.e., stimuli weaker than a certain threshold do not induce AP, whereas overthreshold stimuli trigger the signal with constant amplitude (Trebacz et al. 2006). AP is induced by non-damaging irritations (Trebacz et al. 2006); in particular, it is induced by electric currents (Krol et al. 2006; Bulychev and Krupenina 2010; Sevriukova et al. 2014; Kisnieriene et al., 2016), cooling (Fromm and Bauer 1994; Opritov et al. 2004; Krol et al. 2006), touch (Sibaoka 1991; Shepherd et al. 2008; Degli Agosti 2014), some chemical agents (Felle and Zimmermann 2007), and changes in the light regime (Trebacz and Sievers 1998; Pikulenko and Bulychev 2005). AP is generally propagating through living tissues only, its propagation has constant velocity which usually equals to 0.1–10.0 cm s^{-1} in plants of different species (Sibaoka 1991; Trebacz et al. 2006; Beilby 2007; Favre and Degli Agosti 2007; Lang and Volkov 2008; Zimmermann et al. 2009; Favre et al. 2011).

AP generation is connected with transitory ion channel activation (Beilby 1982, 1984, 2007; Trebacz et al. 2006; Felle and Zimmermann 2007; Sukhov and Vodeneev 2009) and H^+-ATPase inactivation (Vodeneev et al. 2006; Sukhov and Vodeneev 2009). The process includes the following chain of events (Vodeneev et al. 2006; Sukhov and Vodeneev 2009): irritation → initial depolarization of the electrical potential of plasmalemma to threshold value → activation of potential-dependent Ca^{2+} channels → increase in the Ca^{2+} concentration in the cytoplasm → activation of Ca^{2+}-dependent Cl^- channels and inactivation of H^+-ATPase → increase in Cl^- efflux and H^+ influx → depolarization → inactivation of potential-dependent Ca^{2+} channels → decrease in the Ca^{2+} concentration in the cytoplasm → activation of potential-dependent K^+ channels, reactivation of H^+-ATPase → repolarization of the electrical potential of plasmalemma. It should be noted that AP generation is connected with changes in ion concentrations (Wacke et al. 2003; Trebacz et al. 2006; Felle and Zimmermann 2007; Sukhov and Vodeneev 2009), including increased H^+ and Ca^{2+} concentrations in the cytoplasm and their decreased concentrations in apoplasts. AP is a self-propagating ES (Trebacz et al. 2006; Król et al. 2010; Sukhov et al. 2011). In algae and mosses, AP propagates through homogeneous symplast of body cells (Trebacz et al. 2006); in higher plants, the process is connected with symplast of sieve elements (Fromm and Lautner 2007; Zhao et al. 2015) and (or) symplast of parenchyma cells (Opritov et al. 1991; Sukhov et al. 2011) in vascular bundles.

VP (Fig. 1b) is a unique ES in higher plants (Stahlberg et al. 2006; Vodeneev et al. 2015). It is a long-term (minutes to tens of minutes) electrical reaction with an irregular shape that includes long-term depolarization (long-term decrease in the electric potential difference on plasma membrane) and, in many cases, 'AP-like' spikes

Fig. 1 Action potential **a**, variation potential **b,** and system potential **c** in plants. Changes in the difference of electrical potentials on the inside and outside of the plasma membrane are shown. Redrawn from the works of Fromm and Bauer (1994), Sukhov et al. (2014a), and Zimmermann et al. (2009)



(Vodeneev et al. 2015). VP is induced by local damages (Stahlberg et al. 2006; Vodeneev et al. 2015), including local burning, crushing, and pricking. VP amplitude is proportional to the intensity of the damaging stimulus, and it decreases with increasing distance from the damage zone (Vodeneev et al. 2015). Velocity of VP propagation is not constant ($\sim$mm s^{-1}) (Grams et al. 2009; Vodeneev et al. 2012, Sukhov et al. 2012, 2014a; Gallé et al. 2013), and it also decreases with increasing distance from the zone of irritation (Vodeneev et al. 2012, 2015). It should be noted (Fromm and Lautner 2007) that VP is able to pass through inactive or dead tissues.

Currently, VP is considered a local electrical response that is induced by propagation of a hydraulic signal (Mancuso 1999; Stahlberg et al. 2006), chemical signal (Vodeneev et al. 2015), or a combined signal (Malone, 1994; Vodeneev et al. 2012). A hydraulic signal is a pressure wave that is induced by damage and propagates through a plant (Mancuso 1999; Stahlberg et al. 2006); it is possible that the wave induces VP generation in tissues. An alternative hypothesis is that local damage induces propagation through a plant of a specific wound substance that initiates an electrical response (Vodeneev et al. 2015). The wound substance could be oligosaccharides from broken cell walls (Bishop et al. 1981), systemin (Pearce et al. 1991; Peña-Cortés et al. 1995), jasmonate (Farmer and Ryan 1990; Hlavinka et al. 2012), ethylene (O'Donnell et al. 1996), abscisic acid (Leon et al. 2001), or H_2O_2 (Vodeneev et al. 2015). In addition, there are two combined hypotheses: (i) damage-induced increase of pressure induces water flow, transporting wound substance (Malone 1994); and (ii) this pressure change stimulates turbulent diffusion of the wound substance (Vodeneev et al. 2012, 2015; Sukhov et al. 2013a). All potential mechanisms are connected with the xylem of vascular bundles (Vodeneev et al. 2015).

VP generation is mainly connected with H^+-ATPase inactivation (Julien et al. 1991; Stahlberg et al. 2006; Fromm and Lautner 2007; Vodeneev et al. 2015); however, Ca^{2+}, Cl^-, and K^+ channel activation might also participate in the process (Vodeneev et al. 2011, 2015; Sukhov et al. 2013a; Katicheva e al. 2014, 2015; Zhao et al. 2014). Previously, we suggested the following scheme of VP generation and propagation (Vodeneev et al. 2015): local damage → propagation of chemical and (or) hydraulic signals → activation of mechanosensitive and (or) ligand-dependent Ca^{2+} channels → increase in the Ca^{2+} concentration in the cytoplasm → inactivation of H^+-ATPase → long-term depolarization → activation of potential-dependent Ca^{2+} channels → subsequent increase in the Ca^{2+} concentration in the cytoplasm → activation of Ca^{2+}-dependent Cl^- channels → 'AP-like' spikes → time-dependent gradual decrease in the hydraulic and (or) chemical factor action → inactivation of mechanosensitive and (or) ligand-dependent Ca^{2+} channels → decrease in the Ca^{2+} concentration in the cytoplasm → repolarization of the plasmalemma. VP generation is accompanied with changes in H^+ and, probably, Ca^{2+} concentrations (Vodeneev et al. 2011, 2015; Sukhov et al. 2013a; Kaiticheva et al. 2014, 2015). In particular, VP generation is connected with pH decrease in the cytoplasm and pH increase in apoplast (Zimmermann and Felle 2009; Grams et al. 2009; Sukhov et al. 2014a; Sherstneva et al. 2015).

It should be noted that the mechanisms of VP and AP generation are fundamentally similar (Vodeneev et al. 2015), and differences in AP and VP properties are connected with different potential mechanisms of their propagation. However, recently, ESs were associated with another generation mechanism: SP (Zimmermann et al. 2009). SP (Fig. 1c) represents transitory hyperpolarization (increase in the electric potential difference on plasma membrane), which is self-propagated (0.9–1.7 mm c^{-1}) and is connected with H^{+}-ATPase activation (Zimmermann et al. 2009). A few works have demonstrated the propagation of transitory hyperpolarization after different stimulations (Fromm and Eshrich 1993; Lautner et al. 2005; Zimmermann et al. 2009; Fromm et al. 2013). However, the mechanisms of the SP are unclear. There is a hypothesis that SP is connected with H_2O_2 propagation (Suzuki and Mittler 2012); however, this requires further experimental investigation.

ESs induce various physiological responses in plants (Fromm and Lautner 2007; Gallé et al. 2015). ESs increase whole-plant resistance to stressors (Retivin et al. 1997; Sukhov et al. 2015b); induce the expression of pin2 genes (Peña-Cortés et al. 1995; Stanković and Davies 1996; Fisahn et al. 2004); inhibit protein synthesis (Fromm and Lautner 2007); stimulate the production of abscisic and jasmonic acids, systemin and ethylene (Dziubinska et al. 2003; Fisahn et al. 2004; Hlaváčková et al. 2006; Hlavinka et al. 2012; Mousavi et al. 2013); activate respiration (Dziubinska and Trêbacz 1989; Filek and Kościelniak 1997; Sukhov et al. 2012, 2014a; Lautner et al. 2014); change transpiration and stomata opening (Koziolek et al. 2004; Grams et al. 2007; Sukhov et al. 2012, 2015b); suppress metabolite loading into the phloem (Fromm 1991; Fromm and Bauer 1994) and reduce phloem mass flow (Furch et al. 2010); decrease elongation growth of the stem (Fromm and Lautner 2007); regulate leaf movement (Sibaoka 1991; Volkov et al. 2008a, b); and induce cessation of cytoplasmic streaming (Fromm and Lautner 2007). Numerous works show that local irritations and, probably, irritation-induced ESs influence photosynthesis (Peña-Cortés et al. 1995; Koziolek et al. 2004; Hlaváčková et al. 2006; Krupenina and Bulychev 2007; Grams et al. 2009; Pavlovič et al. 2011; Hlavinka et al. 2012; Sukhov et al. 2012, 2013b, 2014a, b; Fromm et al. 2013).

Question about the similarities and differences between the physiological responses induced by different ESs is not clear. The a priori similarity of mechanisms of AP and VP generation suggest that the physiological responses are similar; however, experimental results are contradictory. The responses can be very similar, e.g., AP- and VP-induced respiratory activation (Filek and Kościelniak 1997; Sukhov et al. 2014a; Sherstneva et al. 2015); however, they can be essentially different, e.g., changes in transpiration induced by flame (VP) and ice water (AP) (Lautner et al. 2005). It is probable that this question requires a separate analysis for each physiological response.

Influence of electrical signals on photosynthesis of plants

Various local irritations can induce different photosynthetic responses in intact parts of plants which are revealed by changes in CO_2 assimilation rate under light conditions (Fig. 2), photochemical quantum yields of PSI and PSII, NPQ, etc. In particular, fast inactivation of photosynthesis (Bulychev et al. 2004; Grams et al. 2009; Pavlovič et al. 2011; Pavlovič and Mancuso 2011; Sukhov et al. 2012), long-term inactivation of photosynthesis (Herde et al. 1999a; Hlaváčková et al. 2006; Sherstneva et al. 2015), and

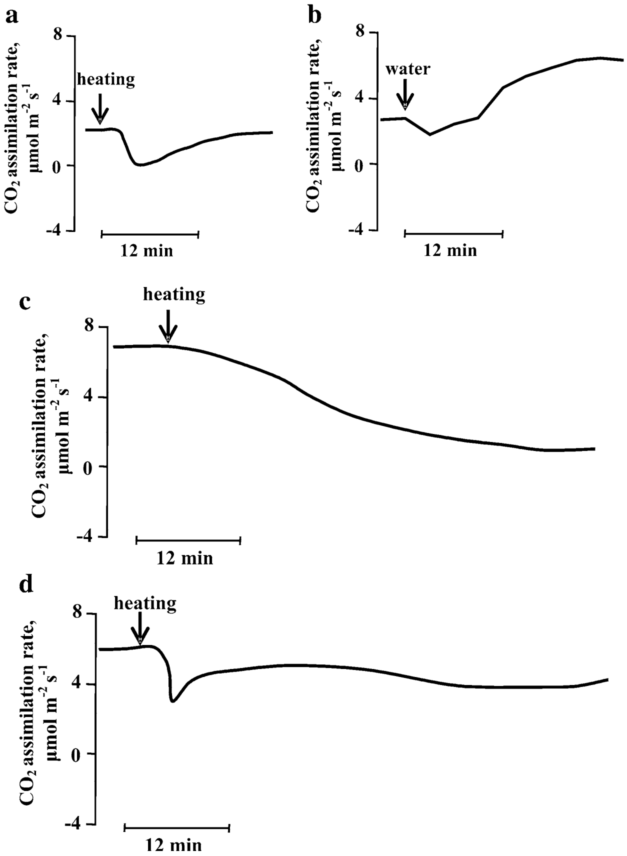


Fig. 2 Local irritation-induced photosynthetic responses which are revealed by changes in CO_2 assimilation rate under light conditions in intact leaves of different plants. **a** Heat-induced fast inactivation of photosynthesis in geranium (redrawn from Sukhov et al. 2012); **b** re-irrigation-induced activation of photosynthesis in maize (redrawn from Fromm and Fei 1998); **c** heat-induced long-term inactivation of photosynthesis in tobacco (redrawn from Hlaváčková et al. 2006); **d** heat-induced combined photosynthetic response in pea which includes fast and long-term inactivation of photosynthesis (redrawn from Sukhov et al. 2015b). Arrows indicate irritation

activation of photosynthesis (Fromm and Fei 1998; Grams et al. 2007) have been observed in intact leaves of plants after local stimulation. Sequences of different types of photosynthetic responses can also be observed (Peña-Cortés et al. 1995; Sukhov et al. 2014b); moreover, the sequence can depend on the type of irritation (Peña-Cortés et al. 1995). Thus, the first fundamental question is 'What is the participation of ESs in each photosynthetic responses?'

Fast inactivation of photosynthesis (Fig. 2a) is the most extensively investigated photosynthetic response. It includes a fast (minutes after stimulation) decrease in the CO_2 assimilation rate under light conditions, lowering of photochemical quantum yields of PSI and PSII, reduction of linear electron flow through photosystems, increased NPQ, and changes in the cyclic electron flow around PSI (Grams et al. 2009; Pavlovič et al. 2011; Sukhov et al. 2012, 2015a). Inactivation of photosynthesis has been shown in Chara algae after current stimulation (Bulychev et al. 2004) and in different higher plants after burning, mechanical wounding, and current stimulation (Herde et al. 1995; Peña-Cortés et al. 1995; Sukhov et al. 2012, 2014a, b, 2015a).

There are several arguments supporting the participation of ESs in the induction of fast inactivation of photosynthesis after irritation. First, the photosynthetic response is absent if ESs do not propagate into leaves or propagate with strongly lowered amplitudes (Sukhov et al. 2012, 2014b). Second, the lag phase before the photosynthetic response increases with the growth of the distance from vascular bundles (potential channels of AP and VP propagation) and from the irritated zone (Lautner et al. 2005; Grams et al. 2009). Third, ice blocks disrupt ES propagation and suppress the development of the response (Gallé et al. 2013). An alternative hypothesis (Grams et al. 2007) supposes that fast inactivation of photosynthesis is connected with hydraulic signals, because this response is absent after the suppression of pressure changes in plants. However, hydraulic signals are connected with VP propagation (Vodeneev et al. 2012, 2015); moreover, suppression of ES propagation by cooling eliminates fast inactivation of photosynthesis (Grams et al. 2007).

What are the ESs that induce fast inactivation of photosynthesis? AP initiates fast inactivation of photosynthesis in Chara algae (Bulychev et al. 2004; Krupenina and Bulychev 2007; Krupenina et al. 2008) and Venus flytrap (Pavlovič et al. 2011; Vredenberg and Pavlovič 2013); VP induces fast inactivation in mimosa (Koziolek et al. 2004), maize (Grams et al. 2009), soybean (Gallé et al. 2013), poplar (Lautner et al. 2005), pea (Sukhov et al. 2014a, b), and geranium (Sukhov et al. 2012). However, cold-induced AP does not influence photosynthesis in poplar (Fromm et al. 2013) and maize leaves (Lautner et al. 2005). Moreover, few works (Hlaváčková et al. 2006; Sherstneva et al. 2015) have demonstrated that fast inactivation of photosynthesis is absent after VP in tobacco and pumpkin. Thus, the influences of ESs on photosynthesis over short time ranges (minutes) have different expressions and can be absent; however, AP- and VP-induced photosynthetic responses are rather similar.

Activation of photosynthesis (Fig. 2b) has been demonstrated in a few works (Fromm and Fei 1998; Grams et al. 2007). They showed that re-irrigation induces AP and increases the CO_2 assimilation rate under light conditions in maize leaves, which starts about 10 min after stimulation and reaches a maximum at 20–30 min. The response is suppressed by the disruption of AP propagation by a cold block (Grams et al. 2007), i.e., AP actually induces the response. Transient activation of photosynthesis could be developed after local action of high temperature (Herde et al. 1995; Peña-Cortés et al. 1995), which is traditionally considered VP-inducing stimulus (Vodeneev et al. 2015); i.e., VP is also capable of inducing activation of photosynthesis.

Only long-term inactivation of photosynthesis (Fig. 2c), including decrease in the CO_2 assimilation rate under light conditions, lowering of photochemical quantum yields of photosystems and increased NPQ, have been observed in tomato (Herde et al. 1999a), tobacco (Hlaváčková et al. 2006), pumpkin (Sukhov et al. 2013b; Sherstneva et al. 2015), and maize (Fromm et al. 2013) after local action of high temperature, mechanical wounding, and current application. This reaction starts at about 2–10 min after stimulation and reaches a peak at 30–40 min. Photosynthesis can be inactivated for up to 5 h or more (Herde et al. 1999a). According to Sherstneva et al. (2015a), the magnitude of long-term inactivation of photosynthesis increases linearly with the growth of VP amplitude, i.e., the ES probably induces the inactivation.

An alternative hypothesis supposes that damage can induce production of systemin, and abscisic and jasmonic acids, which can propagate into the intact parts of the plant and suppress photosynthesis (Peña-Cortés et al. 1995; Hlaváčková et al. 2006; Hlavácková and Naus 2007; Hlavinka et al. 2012). Damage-induced increase in abscisic and jasmonic acids in undamaged parts (Hlaváčková et al. 2006; Hlavinka et al. 2012) and the negative influence of these substances on photosynthesis (Herde et al. 1997; Lovelli et al. 2012) support the hypothesis. However, propagation of an ES into intact leaves (1–2 min after stimulation) precedes the changes in phytohormone contents (more than 10 min) (Hlaváčková et al. 2006; Hlavinka et al. 2012) and electric current application increases abscisic and jasmonic acid concentrations (Herde et al. 1996, 1999a, b). These results show that the following chain of events is also possible: ESs → phytohormones synthesis → long-term inactivation of photosynthesis. The chain can simultaneously explain data associated with abscisic and jasmonic acids (see above) and the dependence of long-term inactivation of photosynthesis on VP amplitude (Sherstneva et al. 2015).

Detailed analysis of AP and VP participation in the induction of long-term inactivation of photosynthesis is lacking. The results of Herde et al. (1999a) showed that long-term inactivation develops after a VP-inducing stimulus (heat treatment) and after a classical AP-inducing stimulus (electric current application). Moreover, the combined photosynthetic response (see examples in Fig. 2d; Herde et al. 1995; Peña-Cortés et al. 1995; Gallé et al. 2013; Sukhov et al. 2014b, 2015b) can differ after AP-inducing and VP-inducing stimuli in 10–15 min range, but the long-term inactivation of photosynthesis was similar after both stimuli (Herde et al. 1995; Peña-Cortés et al. 1995). Thus, I hypothesized that both AP and VP induce long-term inactivation of photosynthesis; however, the connection between ES and the inactivation has been directly investigated only for VP (Sherstneva et al. 2015).

The influences of SP on photosynthesis have not been investigated deeply. There are a few works that show that a hyperpolarization signal (probably SP) can induce fast inactivation of photosynthesis (Lautner et al. 2005) and its long-term inactivation (Fromm et al. 2013); however, the connection of this ES with photosynthetic responses has not been analyzed.

Thus, plant ESs are a probable mechanism of photosynthetic response induction after local irritation. Both AP and VP can induce fast inactivation of photosynthesis, its activation, and long-term inactivation of photosynthesis. It is probable that SP also participates in the induction of photosynthetic changes but the problem has not been investigated thoroughly.

Mechanisms of electrical signals-induced photosynthetic responses in plants

A number of studies have investigated various ways of developing ES-induced inactivation of photosynthesis. The potential mechanisms of fast and long-term inactivation of photosynthesis have been summarized in Fig. 3. The mechanisms of ES-induced activation of photosynthesis have received relatively little attention (see below).

Fast inactivation of photosynthesis

Changes in ion concentrations accompanied with ESs are the probable mechanism of fast inactivation of photosynthesis (Pyatygin et al. 2008). There are two potential mechanisms of induction of inactivation in plants. First, Ca^{2+} concentration increases in the cytoplasm and, later, in chloroplast stroma, are initiators of inactivation of photosynthesis (Krupenina and Bulychev 2007; Bulychev and Komarova 2014). Indeed, AP is initiated by potential-dependent Ca^{2+} channel activation (Felle and Zimmermann 2007; Sukhov and Vodeneev 2009) and VP is probably induced by ligand-dependent and (or) mechanosensitive Ca^{2+} channel activation (Sukhov et al. 2013a; Vodeneev et al. 2015); therefore, influx of calcium ions and increases in the Ca^{2+} concentration in cytoplasm are accompanied with both ESs. Ca^{2+} is transported into chloroplast stroma (Muto et al. 1982; Kreimer et al. 1985); later, an increase in calcium ion concentration can inactivate the Calvin–Benson cycle (Wolosiuk et al. 1993; Johnson et al. 2006), thereby, suppressing the photosynthetic light reactions (see below). The hypothesis of Bulychev and co-workers (Krupenina and Bulychev 2007; Bulychev and Komarova 2014) is supported by the similarity between the change in light dependence of PSII NPQ after AP and that after the action of the Ca^{2+} ionophore (A23187) in Chara algae; in contrast, changes in the light dependence after the application of protonophore (nigericin) are very different from the changes after AP and A23187.

The second hypothesis supposes that ES-related changes in intra- and extracellular pH are the main mechanisms of fast inactivation of photosynthesis (Grams et al. 2009; Sukhov et al. 2013b; 2014a; Sherstneva et al. 2016). H^+-ATPase inactivation plays the main role in VP generation (Sukhov et al. 2013a; Katicheva et al. 2014; Vodeneev et al. 2015) and participates in AP development (Vodeneev et al. 2006; Sukhov and Vodeneev 2009). The inactivation induces a pH increase in the apoplast (0.2–0.7 pH unit) and a pH decrease in the cytoplasm (0.3–0.6 pH unit) (Grams et al. 2009; Sukhov et al. 2014a; Sherstneva et al. 2015, 2015b). Another potential mechanism of the pH changes is Ca^{2+}-dependent Cl^- channel activation during AP (Felle and Zimmermann 2007; Sukhov and Vodeneev 2009) and VP (Sukhov et al. 2013a; Katicheva et al. 2014; Vodeneev et al. 2015), and efflux of chlorine ions, because changes in the Cl^- concentration could be connected with changes in extracellular pH (Felle and Zimmermann 2007; Zimmermann and Felle 2009). Moreover, ES-connected K^+ efflux (Felle and Zimmermann 2007; Vodeneev et al. 2015) could also influence the apoplastic pH because its fixed negative charges can concurrently bind H^+ and K^+ (Gradmann 2001; Sukhov and Vodeneev 2009) (this pathway is not shown in Fig. 3). There are several arguments supporting the participation of pH changes in inactivation of photosynthesis: (1) induction of proton flux into cell reduces the photochemical quantum yields of PSI and PSII (Φ_{PSI} and Φ_{PSII}) and stimulates NPQ in pea leaves similarly to VP-induced photosynthetic response (Sukhov et al. 2014a); (2) pH decrease in perfusion solution increases NPQ in Chara algae (Bulychev et al. 2013); (3) acidification of incubation

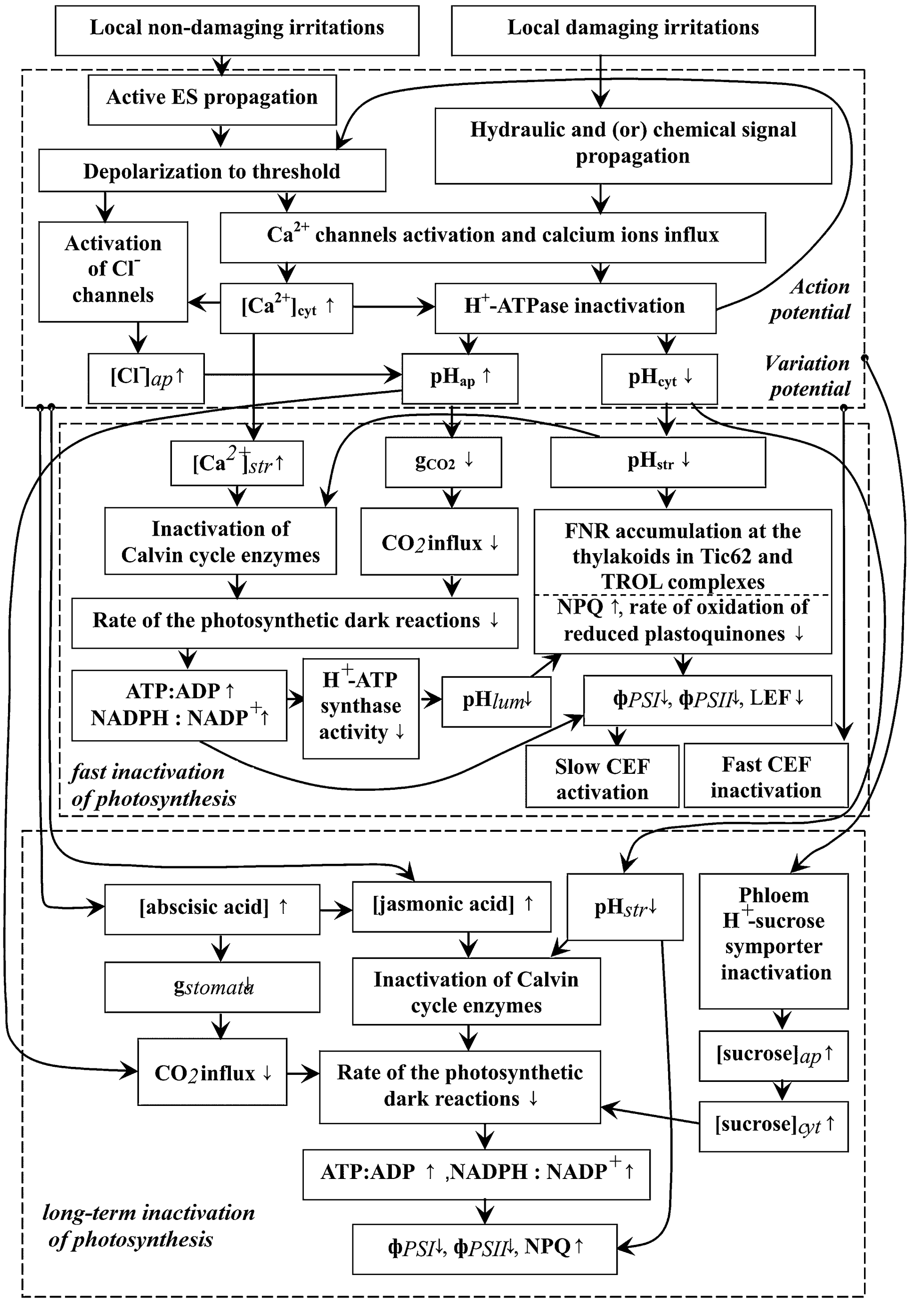


Fig. 3 Schema of the probable pathways of fast and long-term inactivation of photosynthesis induced by electrical signals. Abbreviations: g_{CO_2} is the conductance for CO$_2$ diffusion in the leaf mesophyll; $g_{stomata}$ is the stomata conductance; Φ_{PSI} and Φ_{PSII} are the photochemical quantum yields of PSI and PSII; NPQ is the non-photochemical quenching; LEF and CEF are photosynthetic linear flow and cyclic electron flow around PSI, respectively; FNR is ferredoxin-NADP$^+$ reductase, indices 'ap', 'cyt', 'str', and 'lum' indicate the apoplast, cytoplasm, chloroplast stroma, and lumen, respectively. *Up* and *down arrows* indicate an increase and decrease of a process or parameter, respectively. The processes from the scheme are described in detail in the 'Mechanisms of electrical signals-induced photosynthetic responses in plants' section

medium reduces photochemical quantum yields of photosystems and increases NPQ in pea and pumpkin chloroplasts (Sukhov et al. 2013b, 2014a; Sherstneva et al. 2015); and (4) VP-accompanied pH changes in peas are correlated strongly with the NPQ and CO$_2$ assimilation rate responses (Sherstneva et al. 2016).

Taking into account the influence of Ca^{2+} influx on H$^+$-ATPase and Ca^{2+}-dependent Cl$^-$ channel activity (Sukhov and Vodeneev 2009; Sukhov et al. 2013a; Vodeneev et al. 2015), a direct calcium effect on photosynthesis and its effect on pH changes are not easily distinguished experimentally. I hypothesize that both mechanisms of fast inactivation of photosynthesis induction could be realized at AP and VP. It is possible that these mechanisms have different contributions in various plants; also, the contribution can depend on ES type, because AP and VP have different durations and dynamics of ion fluxes (Sukhov and Vodeneev 2009; Sukhov et al. 2013a).

Development of fast inactivation of photosynthesis after induction is related to inactivation of the photosynthetic dark reactions. Decrease in the CO$_2$ assimilation rate precedes the decrease in PSII photochemical quantum yields

(Koziolek et al. 2004; Lautner et al. 2005); AP- (Pavlovič et al. 2011) and VP-induced (Sukhov et al. 2008a, 2012, 2014a, b, 2015a; Sherstneva et al. 2016) photosynthesis responses are reduced under low activity of the photosynthetic dark reactions (disrupted leaf gas exchange or low CO_2 concentration). The decrease of CO_2 influx (CO_2 concentration lowering) causes inactivation of photosynthesis, which is similar to that induced by VP (Sukhov et al. 2012, 2014b, 2015a), and the CO_2 assimilation rate is correlated strongly with parameters of the photosynthetic light reactions during the fast response (Sukhov et al. 2012).

There are two potential targets of ESs on the photosynthetic dark reactions: Calvin–Benson cycle enzymes and CO_2 flux into chloroplast stroma. It is probable that Ca^{2+} is transported into stroma and directly inactivates Calvin–Benson cycle enzymes (Krupenina and Bulychev 2007). Potentially, a similar mechanism could also participate in the influence of H^+ on the photosynthetic dark reactions because Calvin–Benson cycle enzyme activities are controlled by stroma pH (Wolosiuk et al. 1993). ESs are accompanied by a decrease in cytoplasmic pH (Grams et al. 2009; Sukhov et al. 2014b; Sherstneva et al. 2015), and this decrease can induce lowering of the chloroplast stroma pH which depends on the cytoplasmic pH (Werdan et al. 1975). However, correlation analysis showed (Sherstneva et al. 2016) that changes in apoplastic pH are strongly connected with the response of the CO_2 assimilation rate; however, changes in intracellular pH correlated weakly with the response; i.e., external pH changes probably induce gas exchange responses. The last result supported the hypothesis of the influence of ESs on CO_2 influx, and agrees with Gallé et al. (2013), who showed that VP decreases the conductance for CO_2 diffusion in the leaf mesophyll. The mechanisms of the influence of the increase in external pH on CO_2 conductance is not clear (Sukhov et al. 2014a); it could be connected with lowering of the CO_2:HCO_3^- ratio (Sherstneva et al. 2015); inactivation of aquaporins (Gallé et al. 2013), which participate in CO_2 transport (Uehlein et al. 2003, 2008) and are regulated by pH (Luu and Maurel 2005); and changes in the activity of carbonic anhydrase (Grams et al. 2009).

It is probable that inactivation of the photosynthetic dark reactions increases ATP:ADP and NADPH:$NADP^+$ ratios in chloroplast stroma (Pavlovič et al. 2011; Sukhov et al. 2012, 2014a, 2015a). ADP concentration decrease can suppress thylakoid H^+-ATPsynthase activity and, therefore, contribute to the decrease of H^+ efflux from lumen and its acidification. The lumen acidification decreases linear electron flow (Kramer et al. 1999; Tikhonov 2013, 2014), i.e., it decreases photochemical quantum yields of photosystems and stimulates NPQ (Maxwell and Johnson 2000; Müller et al. 2001). $NADP^+$ concentration decrease also decreases linear electron flow (Pavlovič et al. 2011) and reduces PSI and PSII photochemical quantum yields. Decrease of linear electron flow contributes to the oxidation of the PSI donor side ([$P700^+$] increase), which induces activation of cyclic electron flow around PSI (Golding and Johnson 2003; Miyake et al. 2005; Huang et al. 2012; Zivcak et al. 2013; Sukhov et al. 2015a).

Detailed analysis of ES-induced changes in the parameters of photosynthetic light reactions showed that the changes could be developed without the inactivation of photosynthetic dark reactions (Sukhov et al. 2012, 2014a, b, 2015a; Vredenberg and Pavlovič 2013; Sherstneva et al. 2016), i.e., ESs can also influence the photosynthetic light reactions through other pathways. The following arguments support this influence: (i) VP-induced changes in photochemical quantum yields of PSI and PSII, NPQ, linear electron flow and cyclic electron flow around PSI could be observed under full suppression of CO_2 assimilation inactivation (Sukhov et al. 2012, 2014a, b, 2015a); (ii) AP changed the PSII fluorescence induction curve in about 0.2–1.0 s after the start of illumination (Vredenberg and Pavlovič 2013); (iii) VP-induced dynamics of CO_2 assimilation rate and NPQ could be distinguished (Sukhov et al. 2014a; Sherstneva et al. 2016).

Pathways by which ESs could influence the photosynthetic light reactions without inactivation of the dark reactions are not fully clear. One of them is probable to be connected with chloroplast stroma acidification which can be induced by ES-accompanying pH decrease in the cytoplasm, because protons can enter the stroma, using different H^+-transporting systems in membrane envelope (Peters and Berkowitz 1991; Wu and Berkowitz 1992; Song et al. 2004), and stroma pH depends on the cytoplasmic pH (Werdan et al. 1975). The stroma acidification induces ferredoxin-$NADP^+$ reductase accumulation at the thylakoids in Tic62 and TROL complexes (Alte et al. 2010; Benz et al. 2010), which can disrupt $NADP^+$ reduction and, thereby, suppress electron flow through the acceptor side of PSI. VP-induced decrease of electron flow through the PSI acceptor side in geraniums (Sukhov et al. 2012) supports the participation of this effect in the photosynthetic response. Other pathways of ESs influence on the photosynthetic light reactions can not be also excluded.

Long-term inactivation of photosynthesis

The first question related to ES-induced long-term inactivation of photosynthesis is 'Can changes in Ca^{2+} concentration and pH participate in this inactivation?' Taking into account that the duration of plasmalemma Ca^{2+} channel activation is about 30–40 s (Katicheva et al. 2015), the participation of increased Ca^{2+} concentration in the cytoplasm in the induction of long-term inactivation of photosynthesis is not very likely; however, this way cannot be fully disproved. Alternatively, the duration of AP- and VP-induced pH changes can be tens of minutes in the cytoplasm (Felle and Zimmermann 2007; Sukhov et al. 2014a; Sherstneva et al. 2016) and apoplast (Felle and Zimmermann 2007; Zimmermann and Felle 2009); the dynamics of apoplastic pH increase can be multi-phasic. The results show that ES-induced long-term inactivation could be caused by pH changes in the cytoplasm and apoplast. The mechanisms of influence of pH changes on photosynthesis are probably similar to the mechanisms of fast inactivation (see above).

However, long-term inactivation of photosynthesis can be observed up to 5 h after irritation (Herde et al. 1999a), which is essentially longer that the duration of the pH changes. Local irritation and, probably, ESs (see 'Influence of electrical signals on photosynthesis in plants' for detail) can increase abscisic and jasmonic acid concentrations in intact part of plants (Peña-Cortés et al. 1995; Herde et al. 1996, 1999a, b; Hlaváčková et al. 2006; Hlavácková and Naus 2007; Hlavinka et al. 2012). The increase starts about 8 min (abscisic acid) and 15 min (jasmonic acid) after irritation (Hlaváčková et al. 2006), and could be observed up to 5–6 h after that (Herde et al. 1996, 1999a, b). Abscisic and jasmonic acids inactivate photosynthesis (Herde et al. 1997; Lovelli et al. 2012); moreover, Hlaváčková et al. (2006) showed that concentrations of abscisic and jasmonic acids are linearly associated with CO_2 assimilation during VP-induced long-term inactivation of photosynthesis. Thus, it was hypothesized that increases in abscisic and jasmonic acid concentrations participate in long-term inactivation of photosynthesis after irritation (Hlaváčková et al. 2006; Hlavinka et al. 2012). Investigation of abscisic acid-deficient mutants (Hlavinka et al. 2012) showed that abscisic acid inactivates CO_2 assimilation, decreasing stomata conductance and CO_2 influx, and the jasmonic acid reduces the activities of Calvin–Benson cycle enzymes; both ways can change photosynthesis independently.

Additional mechanisms of development of ES-induced long-term inactivation of photosynthesis are also possible. I speculate that an ES-induced decrease in sugar transport from mesophyll cells to phloem sieve elements can also suppress photosynthesis. It is known that ESs can reduce phloem translocation (Fromm 1991; Fromm and Bauer, 1994; Furch et al. 2010), and restricting sucrose transport from leaves decreases photosynthetic activity (Ainsworth and Bush 2011). Taking into account that (i) ESs are observed in phloem sieve elements (Fromm and Lautner 2007), (ii) the duration of changes in electrical potential (Sukhov et al. 2012, 2014b) and increase of apoplastic pH (Felle and Zimmermann 2007; Zimmermann and Felle 2009) can be tens of minutes, (iii) H^+-sucrose symporter plays a key role in the apoplastic loading of sieve elements (Lalonde et al. 1999), and (iv) an increase in apoplastic pH and depolarization of plasma membrane can decrease activity of the H^+-sucrose symporter (Sukhov et al. 2013c); I hypothesize that ES-induced suppression of H^+-sucrose symporter activity also participates in long-term inactivation of photosynthesis.

Activation of photosynthesis

Mechanisms of ES-induced activation of photosynthesis (increase of CO_2 assimilation under light conditions in 10–30 min after irritation) (Herde et al. 1995; Peña-Cortés et al. 1995; Fromm and Fei 1998; Grams et al. 2007) are currently unclear. Our early theoretical analysis (Sukhov et al. 2008b) showed that a decrease in thylakoid membrane ions permeability could be a potential mechanism of activation of photosynthesis after ESs; however, experimental data concerning the influence of ESs on this permeability are lacking. Thus, mechanisms of ES-induced activation of photosynthesis require further investigations.

Influence of electrical signals on resistance of photosynthetic machinery to stressors

The influence of ESs on photosynthesis supports the hypothesis that the ES-induced responses play important roles in plants. As described in the last section, ESs inactivate the photosynthetic dark reactions (Pavlovič et al. 2011; Sukhov et al. 2012, 2014a, b, 2015a; Gallé et al. 2013), which can cause an increased ATP concentration in chloroplast stroma (Pavlovič et al. 2011; Sukhov et al. 2014a) and stimulates NPQ (Krupenina et al. 2008; Pavlovič et al. 2011; Sukhov et al. 2012, 2014a) and cyclic electron flow around PSI (Sukhov et al. 2015a). NPQ is a mechanism of PSII protection from excess light under stress conditions (Müller et al. 2001; Roach and Krieger-Liszkay 2014); moreover, decreasing the PSII activity, which is induced by the processes, could contribute to the resistance of PSI to stressors (Sonoike 2011; Tikkanen et al. 2014; Tikkanen and Aro 2014). Increase in the cyclic electron flow around PSI is also a typical photosynthetic response to stressors (Bukhov et al. 1999; Allen 2003; Rumeau et al. 2007; Zhang and Sharkey 2009, Sharkey and Zhang 2010; Johnson 2011; Sonoike 2011; Roach and Krieger-Liszkay 2014), which supports the transthylakoid pH difference and ATP synthesis, contributes to regulated energy dissipation in PSII, oxidizes the acceptor side of PSI, and controls reactive oxygen species production, thereby protecting the photosynthetic machinery. Finally, according to Allakhverdiev et al. (2005, 2008), ATP stimulates PSII repair processes under stressor action and

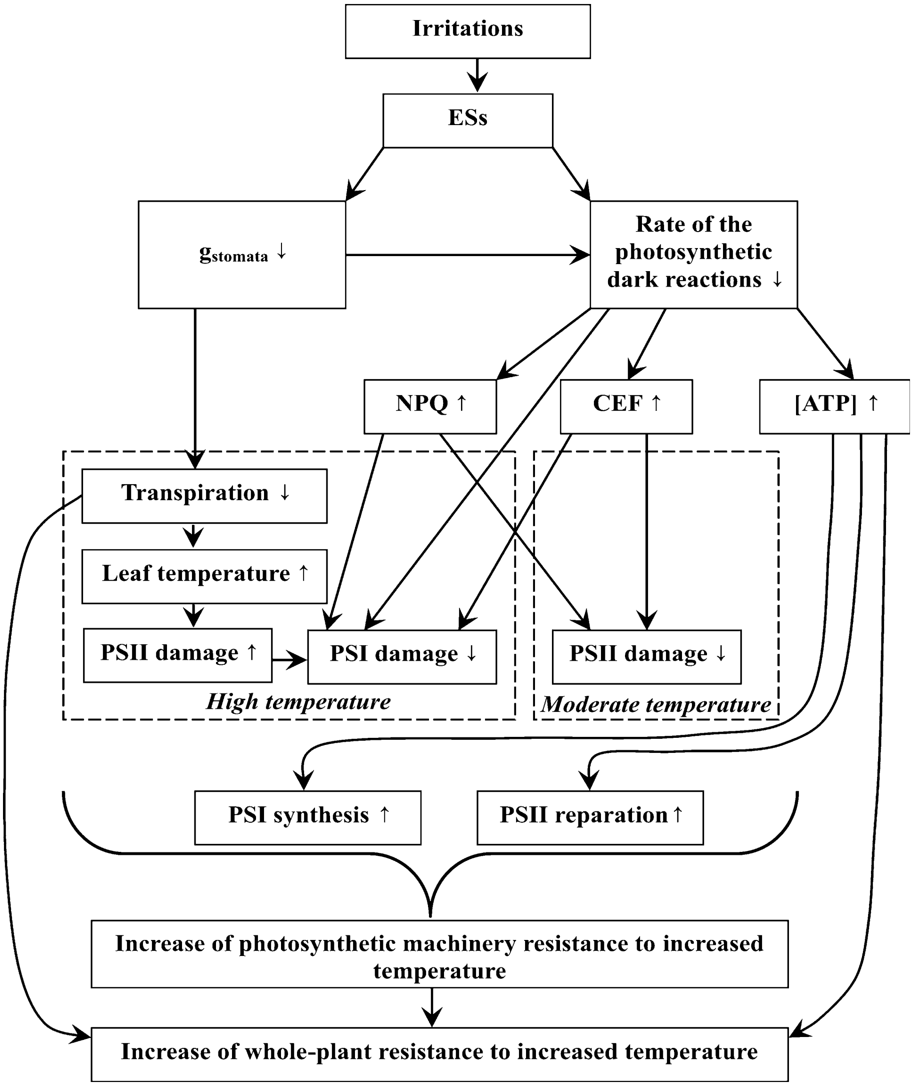


Fig. 4 Schema of the probable pathways of the influence of electrical signals (ESs) on resistance of the photosynthetic machinery and whole plant to increased temperature. *Up* and *down* arrows indicate increase and decrease of process or parameter, respectively. The processes from the scheme are described in detail in the 'Influence of electrical signals on resistance of photosynthetic machinery to stressors' section. g_{stomata}, stomata conductance; *NPQ* non-photochemical quenching, *CEF* photosynthetic cyclic electron flow around PSI, *ATP* ATP concentration in the leaf

after that. Thus, inactivation of the photosynthetic dark reactions induces processes that protect the photosynthetic machinery and contribute its reparation; the processes can explain the positive influence of the inactivation on the resistance of PSI and PSII to increased temperature (Sukhov et al. 2014b). Moreover, inactivation of the photosynthetic dark reactions also participates in the regulation of reactive oxygen species production, stimulating H_2O_2 synthesis (Kim and Portis 2004). It is known that moderate stimulation of reactive oxygen species production can regulate gene expression (Foyer and Noctor 2009, Fischer et al. 2013). In particular, increase of H_2O_2 content can activate expression of genes participating in abiotic stress tolerance (Uchida et al. 2002; Hossain et al. 2015), including genes of heat shock proteins.

Thus, it is very probable that ESs increase the resistance of photosynthetic machinery to stressors. Indeed, AP induced an increase of PSII resistance to cold (−8 °C, 25) and increased temperature (+45 °C, 10 min) after ES induction, and stimulates the repair process after the actions of stressors (Retivin et al. 1999a). VP decreased PSI damage and increased PSII damage under high temperature (temperature increases to +53 °C, 30 min) (Sukhov et al. 2014b, 2015b).

There are two potential reasons for these differences in the influence of ESs on resistance of the photosynthetic machinery to increased temperature. First, it could be related to the different ESs (AP and VP) inducing changes in the photosynthetic machinery. However, both AP and VP suppress the photosynthetic dark reactions, stimulate NPQ and, probably, increase ATP concentration in plants (Pavlovič et al. 2011; Sukhov et al. 2012, 2014a; Sherstneva et al. 2015). AP's influence on cyclic electron flow around PSI has not been investigated; however, VP-induced activation of this flow is mainly connected with the inactivation of the photosynthetic dark reactions (Sukhov et al. 2015a) and the inactivation developed after AP (Pavlovič et al. 2011); i.e., AP-induced stimulation of the cyclic flow around PSI is probable. Thus, I suppose that AP and VP effect similar changes in photosynthetic machinery resistance; however, this supposition requires further investigation. Using of different temperatures (moderate or high) can be an alternative reason of different influence of ESs on photosynthetic machinery. It has been shown (Sukhov et al. 2014b, 2015b) that the positive influence of VP on PSI resistance to increased temperature was observed in leaves under temperature rise to 45–47 °C (temperature of leaf surface), but is absent under its rise to 43 °C.

The positive influence of VP on PSI resistance to high temperature is connected strongly with inactivation of the photosynthetic dark reactions, which is supported by the suppression of VP-induced photosynthetic response and PSI resistance increase under inactivation of the photosynthetic dark reactions (lack of Rubisco carboxylation as a result of low CO_2 concentration) and the similarity between CO_2 lowering- and VP-induced changes in photosynthesis and PSI resistance (Sukhov et al. 2014b). Growth of PSII damage under high temperature is mainly caused by VP-induced stomatal closing, which is caused by H^+-ATPase inactivation (Sukhov et al. 2015b). The closing decreases the transpiration rate under heating and, thereby, increases leaf temperature (Sukhov et al. 2015b). It should be noted that VP-induced intensification of PSII damage under high temperature can contribute to PSI resistance, because lowering the PSII activity decreases the electron flow to PSI and protects this photosystem from damage (Tjus et al. 1998; Sonoike 2011; Tikkanen et al. 2014; Tikkanen and Aro, 2014). Our analysis showed (Surova et al. 2016) that negative correlations are observed between PSI and PSII damage after the action of increased temperature. The mechanisms of the positive influence of AP on PSII resistance to moderate temperature have not been investigated; however, they are probably connected with the photosynthetic response (e.g., stimulation of NPQ and increase of cyclic electron flow around PSI).

Repair of PSII is an important process that supports photosynthetic activity after the actions of different stressors (Nath et al. 2013). Retivin et al. (1999a) showed that AP could also stimulate PSII repair. PSI is weakly repaired (Sonoike 2011; Tikkanen et al. 2014), but its de novo synthesis also participates in the recovery of photosynthetic activity after the actions of stressors. It is probable that an increased ATP concentration contributes to both the processes. The connection between photosynthetic responses and changes in ATP concentration have not been investigated thoroughly; however, both AP and VP can increase the ATP content in phloem exudates (Retivin et al. 1999b), and ATP concentration changes show multi-phasic dynamics (Pyatygin et al. 2008).

We presume that the final result of changes in the resistance of the photosynthetic machinery is increased whole-plant resistance, which is observed after AP (Retivin et al. 1997) and VP (Sukhov et al. 2015b). ES-induced decrease in transpiration (Sukhov et al. 2012, 2015b) and the increase of the ATP content in plants (Retivin et al. 1999b) could also contribute to the increased plant resistance. Figure 4 summarizes the potential influence pathways of ESs on plant resistance to increased temperature. It is probable that the influence of ESs on resistance to other stressors has similar mechanisms; however, this requires further investigation.

Conclusion

Our review shows that local irritation-induced ESs can influence photosynthesis in the intact leaves of plants, including fast and long-term inactivation of photosynthesis and activation of photosynthesis. Fast inactivation of photosynthesis can be caused by Ca^{2+} and (or) H^+ influxes, whereas long-term inactivation may be connected with these influxes, production of abscisic and jasmonic acids, and inactivation of H^+-sucrose symporters. Further photosynthetic inactivation is mainly connected with the inactivation of the photosynthetic dark reactions, which changes the light reactions; however, other pathways of ESs influence on the photosynthetic light reactions are also probable. The mechanisms of ES-induced activation of photosynthesis require further investigation. It is possible that changes in the resistance of the photosynthetic machinery to stressors, including increased temperature, are caused by the ES-induced photosynthetic responses. Protection of the photosynthetic machinery and the whole plant from stressors is probably the result of these changes. Thus, ESs participate in photosynthesis regulation in the whole plant after the local action of stressors.

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References

Ainsworth EA, Bush DR (2011) Carbohydrate export from the leaf: a highly regulated process and target to enhance photosynthesis and productivity. Plant Physiol 155:64–69

Allakhverdiev SI, Nishiyama Y, Takahashi S, Miyairi S, Suzuki I, Murata N (2005) Systematic analysis of the relation of electron transport and ATP synthesis to the photodamage and repair of photosystem II in Synechocystis. Plant Physiol 137:263–273

Allakhverdiev SI, Kreslavski VD, Klimov VV, Los DA, Carpentier R, Mohanty P (2008) Heat stress: an overview of molecular responses in photosynthesis. Photosynth Res 98:541–550

Allen JF (2003) Cyclic, pseudocyclic and noncyclic photophosphorylation: new links in the chain. Trends Plant Sci 8:15–19

Alte F, Stengel A, Benz JP, Petersen E, Soll J, Groll M, Bölter B (2010) Ferredoxin: NADPH oxidoreductase is recruited to thylakoids by binding to a polyproline type II helix in a pH-dependent manner. Proc Natl Acad Sci USA 107:19260–19265

Beilby MJ (1982) $C1^-$ channels in Chara. Philos Trans R Soc London B 299:435–445

Beilby MJ (1984) Calcium and plant action potentials. Plant Cell Environ 7:415–421

Beilby MJ (2007) Action potential in charophytes. Int Rev Cytol 257:43–82

Benz JP, Stengel A, Lintala M, Lee YH, Weber A, Philippar K, Gügel IL, Kaieda S, Ikegami T, Mulo P, Soll J, Bölter B (2010) Arabidopsis Tic62 and ferredoxin-NADP(H) oxidoreductase form light-regulated complexes that are integrated into the chloroplast redox poise. Plant Cell 21:3965–3983

Bishop PD, Makus DJ, Pearce G, Ryan CA (1981) Proteinase inhibitor inducing factor activity in tomato leaves resides in oligosaccharides enzymically released from cell walls. Proc Natl Acad Sci USA 78:3536–3540

Bukhov NG (2004) Dynamic light regulation of photosynthesis (a review). Russ J Plant Physiol 51:742–753

Bukhov NG, Wiese C, Neimanis S, Heber U (1999) Heat sensitivity of chloroplasts and leaves: Leakage of protons from thylakoids and reversible activation of cyclic electron transport. Photosynth Res 59:81–93

Bulychev AA, Komarova AV (2014) Long-distance signal transmission and regulation of photosynthesis in characean cells. Biochemistry (Moscow) 79: 273–281

Bulychev AA, Krupenina NA (2010) Inactivation of plasmalemma conductance in alkaline zones of chara corallina after generation of action potential. Biochem (Moscow) Suppl Ser A 4:232–239

Bulychev AA, Kamzolkina NA, Luengviriya J, Rubin AB, Müller SC (2004) Effect of a single excitation stimulus on photosynthetic activity and light-dependent pH banding in *Chara* cells. J Membr Biol 202:11–19

Bulychev AA, Alova AV, Rubin AB (2013) Fluorescence transients in chloroplasts of *Chara corallina* cells during transmission of photoinduced signal with the streaming cytoplasm. Russ J Plant Physiol 60:33–40

Davies E, Stankovic B (2006) Electrical signals, the cytoskeleton, and gene expression: a hypothesis on the coherence of the cellular responses to environmental insult. In: Baluška F, Mancuso S, Volkmann D (eds) Communication in plants. Neuronal aspects of plant life. Springer, New York, pp 309–320

Degli Agosti R (2014) Touch-induced action potentials in *Arabidopsis thaliana*. Arch Des Sci 67:125–138

Dziubinska H, Trêbacz K (1989) Zawadzki T The effect of excitation on the rate of respiration in the liverwort *Conocephalum conicum*. Physiol Plant 75:417–423

Dziubinska H, Filek M, Koscielniak J, Trebacz K (2003) Variation and action potentials evoked by thermal stimuli accompany enhancement of ethylene emission in distant non-stimulated leaves of *Vicia faba* minor seedlings. J Plant Physiol 160:1203–1210

Evron Y, Johnson EA, McCarty RE (2000) Regulation of proton flow and ATP synthesis in chloroplasts. J Bioenerg Biomembr 32:501–506

Farmer EE, Ryan CA (1990) Interplant communication—airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves. Proc Natl Acad Sci USA 87:7713–7716

Favre P, Degli Agosti R (2007) Voltage-dependent action potentials in *Arabidopsis thaliana*. Physiol Plant 131:263–272

Favre P, Greppin H, Degli Agosti R (2011) Accession-dependent action potentials in *Arabidopsis*. J Plant Physiol 168:653–660

Felle HH, Zimmermann MR (2007) Systemic signaling in barley through action potentials. Planta 226:203–214

Filek M, Kościelniak J (1997) The effect of wounding the roots by high temperature on the respiration rate of the shoot and propagation of electric signal in horse bean seedlings (*Vicia faba* L. minor). Plant Sci 123:39–46

Fisahn J, Herde O, Willmitzer L, Peña-Cortés H (2004) Analysis of the transient increase in cytosolic Ca^{2+} during the action potential of higher plants with high temporal resolution: requirement of Ca^{2+} transients for induction of jasmonic acid biosynthesis and PINII gene expression. Plant Cell Physiol 45:456–459

Fischer BB, Hideg É, Krieger-Liszkay A (2013) Production, detection, and signaling of singlet oxygen in photosynthetic organisms. Antioxid Redox Signal 18:2145–2162

Foyer CH, Noctor G (2009) Redox regulation in photosynthetic organisms: signaling, acclimation, and practical implications. Antioxid Redox Signal 11:861–905

Fromm J (1991) Control of phloem unloading by action potentials in *Mimosa*. Physiol Plant 83:529–533

Fromm J, Bauer T (1994) Action potentials in maize sieve tubes change phloem translocation. J Exp Bot 45:463–469

Fromm J, Eshrich W (1993) Electric signals released from roots of willow (*Salix viminalis* L.) change transpiration and photosynthesis. J Plant Physiol 141:673–680

Fromm J, Fei H (1998) Electrical signaling and gas exchange in maize plants of drying soil. Plant Sci 132:203–213

Fromm J, Lautner S (2007) Electrical signals and their physiological significance in plants. Plant Cell Environ 30:249–257

Fromm J, Hajirezaei MR, Becker VK, Lautner S (2013) Electrical signaling along the phloem and its physiological responses in the maize leaf. Front Plant Sci 4:239

Furch AC, Zimmermann MR, Will T, Hafke JB, van Bel AJ (2010) Remote-controlled stop of phloem mass flow by biphasic occlusion in Cucurbita maxima. J Exp Bot 61:3697–7308

Gallé A, Lautner S, Flexas J, Ribas-Carbo M, Hanson D, Roesgen J, Fromm J (2013) Photosynthetic responses of soybean (*Glycine max* L.) to heat-induced electrical signalling are predominantly governed by modifications of mesophyll conductance for CO_2. Plant Cell Environ 36:542–552

Gallé A, Lautner S, Flexas J, Fromm J (2015) Environmental stimuli and physiological responses: the current view on electrical signalling. Environ Exp Bot 114:15–21

Golding AJ, Johnson GN (2003) Down-regulation of linear and activation of cyclic electron transport during drought. Planta 218:107–114

Gradmann D (2001) Models for oscillations in plants. Aust J Plant Physiol 28:577–590

Grams TEE, Koziolek C, Lautner S, Matyssek R, Fromm J (2007) Distinct roles of electric and hydraulic signals on the reaction of leaf gas exchange upon re-irrigation in *Zea mays* L. Plant Cell Environ 30:79–84

Grams TEE, Lautner S, Felle HH, Matyssek R, Fromm J (2009) Heat-induced electrical signals affect cytoplasmic and apoplastic pH as well as photosynthesis during propagation through the maize leaf. Plant Cell Environ 32:319–326

Herde O, Fuss H, Peña-Cortés H, Fisahn J (1995) Proteinase inhibitor II gene expression induced by electrical stimulation and control of photosynthetic activity in tomato plants. Plant Cell Physiol 36:737–742

Herde O, Atzorn R, Fisahn J, Wasternack C, Willmitzer L, Pena-Cortes H (1996) Localized wounding by heat initiates the accumulation of proteinase inhibitor ii in abscisic acid-deficient plants by triggering jasmonic acid biosynthesis. Plant Physiol 112:853–860

Herde O, Peña-Cortés H, Willmitzer L, Fisahn J (1997) Stomatal responses to jasmonic acid, linolenic acid and abscisic acid in wiid-type and ABA-deficient tomato plants. Plant Cell Environ 20:136–141

Herde O, Pena Cortes H, Wasternack C, Willmitzer L, Fisahn J (1999a) Electric signaling and pin2 gene expression on different abiotic stimuli depend on a distinct threshold level of endogenous abscisic acid in several abscisic acid-deficient tomato mutants. Plant Physiol 119:213–218

Herde O, Peña-Cortés H, Fuss H, Willmitzer L, Fisahn J (1999b) Effects of mechanical wounding, current application and heat treatment on chlorophyll fluorescence and pigment composition in tomato plants. Physiol Plant 105:179–184

Hlavácková V, Naus J (2007) Chemical signal as a rapid long-distance information messenger after local wounding of a plant? Plant Signal Behav 2:103–105

Hlaváčková V, Krchňák P, Nauš J, Novák O, Špundová M, Strnad M (2006) Electrical and chemical signals involved in short-term systemic photosynthetic responses of tobacco plants to local burning. Planta 225:235–244

Hlavinka J, Nožková-Hlaváčková V, Floková K, Novák O, Nauš J (2012) Jasmonic acid accumulation and systemic photosynthetic and electrical changes in locally burned wild type tomato, ABA-deficient sitiens mutants and sitiens pre-treated by ABA. Plant Physiol Biochem 54:89–96

Hossain MA, Bhattacharjee S, Armin SM, Qian P, Xin W, Li HY, Burritt DJ, Fujita M, Tran LS (2015) Hydrogen peroxide priming modulates abiotic oxidative stress tolerance: insights from ROS detoxification and scavenging. Front Plant Sci 6:420

Huang W, Yang SJ, Zhang SB, Zhang JL, Cao KF (2012) Cyclic electron flow plays an important role in photoprotection for the resurrection plant *Paraboea rufescens* under drought stress. Planta 235:819–828

Johnson GN (2011) Physiology of PSI cyclic electron transport in higher plants. Biochim Biophys Acta 1807:384–389

Johnson CH, Shingles R, Ettinger WF (2006) Regulation and role of calcium fluxes in the chloroplast. In: Wise RR, Hoober JK (eds) The structure and function of plastids. Springer, Dordrecht, pp 403–416

Julien JL, Desbiez MO, de Jaeger G, Frachisse JM (1991) Characteristics of the wave of depolarization induced by wounding in *Bidens pilosa* L. J Exp Bot 42:131–137

Katicheva L, Sukhov V, Akinchits E, Vodeneev V (2014) Ionic nature of burn-induced variation potential in wheat leaves. Plant Cell Physiol 55:1511–1519

Katicheva L, Sukhov V, Bushueva A, Vodeneev V (2015) Evaluation of the open time of calcium channels at variation potential generation in wheat leaf cells. Plant Signal Behav 10:e993231

Kim K, Portis AR Jr (2004) Oxygen-dependent H_2O_2 production by Rubisco. FEBS Lett 571:124–128

Kisnieriene V, Lapeikaite I, Sevriukova O, Ruksenas O (2016) The effects of Ni^{2+} on electrical signaling of *Nitellopsis obtusa* cells. J Plant Res. doi:10.1007/s10265-016-0794-3

Koziolek C, Grams TEE, Schreiber U, Matyssek R, Fromm J (2004) Transient knockout of photosynthesis mediated by electrical signals. New Phytol 161:715–722

Kramer DM, Sacksteder CA, Cruz JA (1999) How acidic is the lumen? Photosynth Res 60:151–163

Kreimer G, Melkonian M, Latzko E (1985) An electrogenic uniport mediates light-dependent Ca^{2+} influx into intact spinach chloroplasts. FEBS Lett 180:253–258

Krol E, Dziubinska H, Stolarz M, Trebacz K (2006) Effects of ion channel inhibitors on cold- and electrically-induced action potentials in *Dionaea muscipula*. Biol Plant 50:411–416

Król E, Dziubiñska H, Trêbacz K (2010) What do plants need action potentials for? In: DuBois ML (ed) Action potential: biophysical and cellular context, initiation, phases and propagation. Nova Science Publishers, New York, pp 1–26

Krupenina NA, Bulychev AA (2007) Action potential in a plant cell lowers the light requirement for non-photochemical energy-dependent quenching of chlorophyll fluorescence. Biochim Biophys Acta 1767:781–788

Krupenina NA, Bulychev AA, Roelfsema MRG, Schreiber U (2008) Action potential in Chara cells intensifies spatial patterns of photosynthetic electron flow and non-photochemical quenching in parallel with inhibition of pH banding. Photochem Photobiol Sci 7:681–688

Lalonde S, Boles E, Hellmann H, Barker L, Patrick JW, Frommer WB, Ward JM (1999) The dual function of sugar carriers transport and sugar sensing. Plant Cell 11:707–726

Lang RD, Volkov AG (2008) Solitary waves in soybean induced by localized thermal stress. Plant Signal Behav 3:224–228

Lautner S, Grams TEE, Matyssek R, Fromm J (2005) Characteristics of electrical signals in poplar and responses in photosynthesis. Plant Physiol 138:2200–2209

Lautner S, Stummer M, Matyssek R, Fromm J, Grams TEE (2014) Involvement of respiratory processes in the transient knockout of net CO_2 uptake in Mimosa pudica upon heat stimulation. Plant Cell Environ 37:254–260

Leon J, Rojo E, Sanchez-Serrano JJ (2001) Wound signalling in plants. J Exp Bot 52:1–9

Lovelli S, Scopa A, Perniola M, Di Tommaso T, Sofo A (2012) Abscisic acid root and leaf concentration in relation to biomass partitioning in salinized tomato plants. J Plant Physiol 169:226–233

Luo HB, Ma L, Xi HF, Duan W, Li SH, Loescher W, Wang JF, Wang LJ (2011) Photosynthetic responses to heat treatments at different temperatures and following recovery in grapevine (*Vitis amurensis* L.) leaves. PLoS One 6:e23033

Luu DT, Maurel C (2005) Aquaporins in a challenging environment: molecular gears for adjusting plant water status. Plant Cell Environ 28:85–96

Malone M (1994) Wound-induced hydraulic signals and stimulus transmission in *Mimosa pudica* L. New Phytol 128:49–56

Mancuso S (1999) Hydraulic and electrical transmission of wound-induced signals in *Vitis vinifera*. Aust J Plant Physiol 26:55–61

Maxwell K, Johnson GN (2000) Chlorophyll fluorescence—a practical guide. J Exp Bot 51:659–668

Miyake C, Miyata M, Shinzaki Y, Tomizawa K (2005) CO_2 response of cyclic electron flow around PSI (CEF-PSI) in tobacco leaves–relative electron fluxes through PSI and PSII determine the magnitude of non-photochemical quenching (NPQ) of Chl fluorescence. Plant Cell Physiol 46:629–637

Mousavi SAR, Chauvin A, Pascaud F, Kellenberger S, Farmer EE (2013) GLUTAMATE RECEPTOR-LIKE genes mediate leaf-to-leaf wound signaling. Nature 500:422–426

Müller P, Li X-P, Niyogi KK (2001) Non-photochemical quenching. A response to excess light energy. Plant Physiol 125:1558–1566

Munekage Y, Hashimoto M, Miyake C, Tomizawa K, Endo T, Tasaka M, Shikanai T (2004) Cyclic electron flow around photosystem I is essential for photosynthesis. Nature 429:579–582

Murata N (2009) The discovery of state transitions in photosynthesis 40 years ago. Photosynth Res 99:155–160

Muto S, Izawa S, Miyachi S (1982) Light-induced Ca^{2+} uptake by intact chloroplasts. FEBS Lett 139:250–254

Nath K, Jajoo A, Poudyal RS, Timilsina R, Park YS, Aro EM, Nam HG, Lee CH (2013) Towards a critical understanding of the photosystem II repair mechanism and its regulation during stress conditions. FEBS Lett 587:3372–3381

O'Donnell PJ, Calvert C, Atzorn R, Wasternack C, Leyser HMO, Bowles DJ (1996) Ethylene as a signal mediating the wound response of tomato plants. Science 274:1914–1917

Opritov VA, Pyatygin SS, Retivin VG (1991) Biolectrogenesis in higher plants. Nauka, Moskow

Opritov VA, Lobov SA, Pyatygin SS, Mysyagin SA (2004) Analysis of possible involvement of local bioelectric responses in chilling perception by higher plants exemplified by *Cucurbita pepo*. Russ J Plant Physiol 52:801–808

Pastenes C, Horton P (1996) Effect of high temperature on photosynthesis in beans (I. Oxygen evolution and chlorophyll fluorescence). Plant Physiol 112:1245–1251

Pavlovič A, Mancuso S (2011) Electrical signaling and photosynthesis. Can they co-exist together? Plant Sign Behav 6:840–842

Pavlovič A, Slováková L, Pandolfi C, Mancuso S (2011) On the mechanism underlying photosynthetic limitation upon trigger hair irritation in the carnivorous plant Venus flytrap (*Dionaea muscipula* Ellis). J Exp Bot 62:1991–2000

Pearce G, Strydom D, Johnson S, Ryan CA (1991) A polypeptide from tomato leaves induces wound-inducible proteinase inhibitor proteins. Science 253:895–898

Peña-Cortés H, Fisahn J, Willmitzer L (1995) Signals involved in wound-induced proteinase inhibitor II gene expression in tomato and potato plants. Proc Natl Acad Sci USA 92:4106–4113

Peters JS, Berkowitz GA (1991) Studies on the system regulating proton movement across the chloroplast envelope. Effects of ATPase inhibitors, Mg^{2+}, and an amine anesthetic on stromal pH and photosynthesis. Plant Physiol 95:1229–1236

Pfannschmidt T, Allen JF, Oelmüller R (2001) Principles of redox control in photosynthesis gene expression. Physiol Plant 112:1–9

Pikulenko MM, Bulychev AA (2005) Light-triggered action potentials and changes in quantum efficiency of photosystem ii in *Anthoceros* cells. Russ J Plant Physiol 52:584–590

Pyatygin SS, Opritov VA, Vodeneev VA (2008) Signaling role of action potential in higher plants. Russ J Plant Physiol 55:285–291

Retivin VG, Opritov VA, Fedulina SB (1997) Generation of action potential induces preadaptation of *Cucurbita pepo* L. stem tissues to freezing injury. Russ J Plant Physiol 44:432–442

Retivin VG, Opritov VA, Lobov SA, Tarakanov SA, Khudyakov VA (1999a) Changes in the resistance of photosynthesizing cotyledon cells of pumpkin seedlings to cooling and heating, as induced by the stimulation of the root system with KCl solution. Russ J Plant Physiol 46:689–696

Retivin VG, Opritov VA, Abramova NN, Lobov SA, Fedulina SB (1999b) ATP level in the phloem exudate of higher plant shoot after propagation of electric responses to the burning or cooling. Vestn Nizhegorod Univ im NI Lobachevskogo, Ser Biol, 124–131

Roach T, Krieger-Liszkay A (2014) Regulation of photosynthetic electron transport and photoinhibition. Curr Protein Pept Sci 15:351–362

Rumeau D, Peltier G, Cournac L (2007) Chlororespiration and cyclic electron flow around PSI during photosynthesis and plant stress response. Plant Cell Environ 30:1041–1051

Sevriukova O, Kanapeckaite A, Lapeikaite I, Kisnieriene V, Ladygiene R, Sakalauskas V (2014) Charophyte electrogenesis as a biomarker for assessing the risk from low-dose ionizing radiation to a single plant cell. J Environ Radioact 136:10–15

Sharkey TD, Zhang R (2010) High temperature effects on electron and proton circuits of photosynthesis. J Integr Plant Biol 52:712–722

Shepherd VA, Beilby MJ, Al Khazaaly SA, Shimmen T (2008) Mechano-perception in Chara cells: the influence of salinity and calcium on touch-activated receptor potentials, action potentials and ion transport. Plant Cell Environ 31:1575–1591

Sherstneva ON, Vodeneev VA, Katicheva LA, Surova LM, Sukhov VS (2015) Participation of intracellular and extracellular pH changes in photosynthetic response development induced by variation potential in pumpkin seedlings. Biochemistry (Moscow) 80:776–784

Sherstneva ON, Surova LM, Vodeneev VA, Plotnikova YI, Bushueva AV, Sukhov VS (2016) The role of the intra- and extracellular protons in the photosynthetic response induced by the variation potential in pea seedlings. Biochem (Moscow) Suppl Ser A 10:60–67

Shikanai T (2014) Central role of cyclic electron transport around photosystem I in the regulation of photosynthesis. Curr Opin Biotechnol 26:25–30

Sibaoka T (1991) Rapid plant movements triggered by action potentials. Bot Mag Tokyo 104:73–95

Song C-P, Guo Y, Qiu Q, Lambert G, Galbraith DW, Jagendorf A, Zhu J-K (2004) A probable Na^{+} (K^{+}) H^{+} exchanger on the chloroplast envelope functions in pH homeostasis and chloroplast development in *Arabidopsis thaliana*. Proc Natl Acad Sci USA 101:10211–10216

Sonoike K (2011) Photoinhibition of photosystem I. Physiol Plant 142:56–64

Stahlberg R, Cleland RE, van Volkenburgh E (2006) Slow wave potentials—a propagating electrical signal unique to higher plants. In: Baluška F, Mancuso S, Volkmann D (eds) Communication in plants. Neuronal aspects of plant life. Springer, New York, pp 291–308

Stanković B, Davies E (1996) Both action potentials and variation potentials induce proteinase inhibitor gene expression in tomato. FEBS Lett 390:275–279

Sukhov V, Vodeneev V (2009) A mathematical model of action potential in cells of vascular plants. J Membr Biol 232:59–67

Sukhov VS, Pyatygin SS, Opritov VA, Krauz VO (2008a) Influence of propagating electrical signals on delayed luminescence in pelargonium leaves: theoretical analysis. Biophysics 53:308–312

Sukhov VS, Pyatygin SS, Opritov VA, Krauz VO (2008b) Influence of propagating electrical signals on delayed luminescence in pelargonium leaves: experimental analysis. Biophysics 53:226–228

Sukhov V, Nerush V, Orlova L, Vodeneev V (2011) Simulation of action potential propagation in plants. J Theor Biol 291:47–55

Sukhov V, Orlova L, Mysyagin S, Sinitsina J, Vodeneev V (2012) Analysis of the photosynthetic response induced by variation potential in geranium. Planta 235:703–712

Sukhov V, Akinchits E, Katicheva L, Vodeneev V (2013a) Simulation of variation potential in higher plant cells. J Membr Biol 246:287–296

Sukhov VS, Kalinin VA, Surova LM, Sherstneva ON, Vodeneev VA (2013b) Mathematical simulation of H^{+}-sucrose symporter of plasma membrane in higher plants. Biochem (Moscow) Suppl Ser A 7:163–169

Sukhov VS, Surova LM, Sherstneva ON, Rumyantsev EA, Vodeneev VA (2013c) Influence of a variation potential on photosynthesis in pumpkin seedlings (*Cucurbita pepo* L.). Biophysics 58:361–365

Sukhov V, Sherstneva O, Surova L, Katicheva L, Vodeneev V (2014a) Proton cellular influx as a probable mechanism of variation potential influence on photosynthesis in pea. Plant Cell Environ 37:2532–2541

Sukhov V, Surova L, Sherstneva O, Vodeneev V (2014b) Influence of variation potential on resistance of the photosynthetic machinery to heating in pea. Physiol Plant 152:773–783

Sukhov V, Surova L, Sherstneva O, Bushueva A, Vodeneev V (2015a) Variation potential induces decreased PSI damage and increased PSII damage under high external temperatures in pea. Funct Plant Biol 42:727–736

Sukhov V, Surova L, Sherstneva O, Katicheva L, Vodeneev V (2015b) Variation potential influence on photosynthetic cyclic electron flow in pea. Front Plant Sci 5:766

Surova L, Sherstneva O, Vodeneev V, Sukhov V (2016) Variation potential propagation decreases heat-related damage of pea photosystem I by 2 different pathways. Plant Sign Behav 11:e1145334

Suzuki N, Mittler R (2012) Reactive oxygen species-dependent wound responses in animals and plants. Free Radic Biol Med 53:2269–2276

Tikhonov AN (2013) pH-dependent regulation of electron transport and ATP synthesis in chloroplasts. Photosynth Res 116:511–534

Tikhonov AN (2014) The cytochrome b6f complex at the crossroad of photosynthetic electron transport pathways. Plant Physiol Biochem 81:163–183

Tikkanen M, Aro EM (2014) Integrative regulatory network of plant thylakoid energy transduction. Trends Plant Sci 19:10–17

Tikkanen M, Mekala NR, Aro EM (2014) Photosystem II photoinhibition-repair cycle protects Photosystem I from irreversible damage. Biochim Biophys Acta 1837:210–215

Tjus SE, Møller BL, Scheller HV (1998) Photosystem I is an early target of photoinhibition in barley illuminated at chilling temperatures. Plant Physiol 116:755–764

Trebacz K, Sievers A (1998) Action potentials evoked by light in traps of *Dionaea muscipula* Ellis. Plant Cell Physiol 39:369–372

Trebacz K, Dziubinska H, Krol E (2006) Electrical signals in long-distance communication in plants. In: Baluška F, Mancuso S, Volkmann D (eds) Communication in plants. Neuronal aspects of plant life. Springer, New York, pp 277–290

Uchida A, Jagendorf AT, Hibino T, Takabe T, Takabe T (2002) Effects of hydrogen peroxide and nitric oxide on both salt and heat stress tolerance in rice. Plant Sci 163:515–523

Uehlein N, Lovisolo C, Siefritz F, Kaldenhoff R (2003) The tobacco aquaporin NtAQP1 is a membrane CO_2 pore with physiological functions. Nature 425:734–737

Uehlein N, Otto B, Hanson DT, Fischer M, McDowell N, Kaldenhoff R (2008) Function of Nicotiana tabacum aquaporins as chloroplast gas pores challenges the concept of membrane CO_2 permeability. Plant Cell 20:648–657

Vodeneev VA, Opritov VA, Pyatygin SS (2006) Reversible changes of extracellular pH during action potential generation in a higher plant *Cucurbita pepo*. Russ J Plant Physiol 53:481–487

Vodeneev VA, Akinchits EK, Orlova LA, Sukhov VS (2011) The role of Ca^{2+}, H^+, and Cl^- ions in generation of variation potential in pumpkin plants. Russ J Plant Physiol 58:974–981

Vodeneev V, Orlova A, Morozova E, Orlova L, Akinchits E, Orlova O, Sukhov V (2012) The mechanism of propagation of variation potentials in wheat leaves. J Plant Physiol 169:949–954

Vodeneev V, Akinchits E, Sukhov V (2015) Variation potential in higher plants: mechanisms of generation and propagation. Plant Signal Behav 10:e1057365

Volkov AG, Adesina T, Markin VS, Jovanov E (2008a) Kinetics and mechanism of Dionaea muscipula trap closing. Plant Physiol 146:694–702

Volkov AG, Coopwood KJ, Markin VS (2008b) Inhibition of the *Dionaea muscipula* Ellis trap closure by ion and water channels blockers and uncouplers. Plant Sci 175:642–649

Vredenberg W, Pavlovič A (2013) Chlorophyll a fluorescence induction (Kautsky curve) in a Venus flytrap (*Dionaea muscipula*) leaf after mechanical trigger hair irritation. J Plant Physiol 170:242–250

Wacke M, Thiel G, Hütt MT (2003) Ca^{2+} dynamics during membrane excitation of green alga Chara: model simulations and experimental data. J Membr Biol 191:179–192

Werdan K, Heldt HW, Milovancev M (1975) The role of pH in the regulation of carbon fixation in the chloroplast stroma. Studies on CO_2 fixation in the light and dark. Biochim Biophys Acta 396:276–292

Wolosiuk RA, Ballicora MA, Hagelin K (1993) The reductive pentose phosphate cycle for photosynthetic CO_2 assimilation: enzyme modulation. FASEB J 7:622–637

Wu W, Berkowitz GA (1992) Stromal pH and photosynthesis are affected by electroneutral K^+ and H^+ exchange through chloroplast envelope ion channels. Plant Physiol 98:666–672

Yamori W, Sakata N, Suzuki Y, Shikanai T, Makino A (2011) Cyclic electron flow around photosystem I via chloroplast NAD(P)H dehydrogenase (NDH) complex performs a significant physiological role during photosynthesis and plant growth at low temperature in rice. Plant J 68:966–976

Zhang R, Sharkey TD (2009) Photosynthetic electron transport and proton flux under moderate heat stress. Photosynth Res 100:29–43

Zhao DJ, Wang ZY, Huang L, Jia YP, Leng JQ (2014) Spatio-temporal mapping of variation potentials in leaves of *Helianthus annuus* L. seedlings in situ using multi-electrode array. Sci Rep 4:5435

Zhao DJ, Chen Y, Wang ZY, Xue L, Mao TL, Liu YM, Wang ZY, Huang L (2015) High-resolution non-contact measurement of the electrical activity of plants in situ using optical recording. Sci Rep 5:13425

Zimmermann MR, Felle HH (2009) Dissection of heat-induced systemic signals: superiority of ion fluxes to voltage changes in substomatal cavities. Planta 229:539–547

Zimmermann MR, Maischak H, Mithoefer A, Boland W, Felle HH (2009) System potentials, a novel electrical long-distance apoplastic signal in plants, induced by wounding. Plant Physiol 149:1593–1600

Zivcak M, Brestic M, Balatova Z, Drevenakova P, Olsovska K, Kalaji HM, Yang X, Allakhverdiev SI (2013) Photosynthetic electron transport and specific photoprotective responses in wheat leaves under drought stress. Photosynth Res 117:529–546