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Environmental stimuli and physiological responses: The current view on electrical signalling

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ABSTRACT

Electrical signals have been studied in numerous species so far. It appears that two main types of such signals occur in plants, rapid action potentials (APs) and slower variation potentials (VPs). While APs are generally evoked by non-invasive stimuli and follow the all-or-nothing principle as in neurons, VPs are mostly triggered by wounding and do not follow the all-or-nothing law. They are correlated to the stimulus strength and last longer than APs. The transmission of both, APs and VPs, occurs via the phloem over long distances and via plasmodesmata over short distances from cell to cell. Regarding physiological functions of electrical signals, numerous examples exist. They regulate rapid leaf movements in order to catch insects and for instance, affect nutrient uptake, gene expression and phloem transport. Recently, it was shown that apart from hydraulic signals, electric signals also play a significant role in root-to-shoot communication of drought-stressed plants. Re-irrigation of plants after soil drying initiates rapid hydraulic as well as electric signalling which affects the gas exchange of leaves. In addition, evidence was found for a link between electrical signals and photosynthesis as well as respiration. Wound-induced VPs cause a transient suppression in photosynthetic activity and an increase in respiratory CO_2 release. The results led us to conclude that different stimulation types trigger characteristic electrical signals each with specific influence on physiological processes.

1. Introduction

Classic work on action potentials in plants already indicates that all higher plants may use electrical signals to regulate various physiological functions (Pickard, 1973). Within the last few years, focus on plant electrophysiology research has strongly shifted from short-distance, uni-cellular towards long-distance, systemic signalling. Remarkably enough, plants also possess most of the chemistry of the neuromotoric system in animals, i.e. neurotransmitters, such as acetylcholine, or cellular messengers, such as calmodulin, or cellular motors, e.g. actin. Further, voltage-gated ion channels as well as sensors for touch, for light, gravity and temperature, have been manifoldly detected in plant physiology research. And yet, despite the cellular equipment, electrical signalling in plants has not reached the great complexity as in nerves. However, a very simple neural network-like signalling pathway has been formed with the phloem tissue, allowing plants to communicate successfully over long distances. The necessity for plants to having developed networks of electrical signalling is most likely due to enable rapid response to environmental stimuli and stress factors. Various stimulations trigger specific electric responses in living plant cells, which then have the ways and means to transmit the signal to a distant responding region. Contrasting chemical signalling, e.g. by phytohormones, electrical signals are able to transmit information over long distances very rapidly: most of the plant action potentials (AP) investigated so far revealed velocities ranging between 0.005 and 0.2 $\mathrm{m\,s^{-1}}$ (Fromm and Lautner, 2007).

Despite all the similarities between animal neuronal systems and plant signalling pathways, it appears to be unlikely that latter was actually adopted from the animal system. Rather we would need to look at unicellular ancestors, which have no need for transmitting signals over long distances, when searching for the common evolutionary roots of action potentials in plants and animals. Consequently, the transfer function of electrical signalling over distances most likely has evolved at a later evolutionary stage, assuming, that during the course of evolution development of plants and animals branched off into different directions. It

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becomes obvious, that both plants and animals inherited their principle neuronal capabilities from their bacterial ancestors, since cellular excitability has been shown to exist in those primitive organisms (Simons, 1992). This has been set out for example for changes in membrane potential during bacterial chemotaxis (Szmelcman and Adler, 1976) or the sensitivity to mechanical touch. Regarding the latter function, pressure-sensitive ion channels are hypothesized to have a principally osmotic function (Martinac et al., 1987). Likewise, for the early formation of action potentials osmotic function might also have been the purpose, as studies on unicellular algae such as *Acetabularia* indicated (Mummert and Gradmann, 1976). But also characean algae have shown to form action potentials, as was shown at a very early stage of plant electrophysiology for *Nitella* in the internodal cells (Hörmann, 1898). Here, the functional resemblance of electrical stimulation to the contraction response displayed by skeletal muscle cells after electrical stimulation by nerve cells was illustrated. Once having left aquasphere and taken over dry land during the course of evolution, requirements on the cellular excitability and signalling capability have also altered. The focus shifted towards working out of survival techniques in order to meet the needs of the new environment, e.g. the development of stomatal guard cell's capacity of prompt responding, or the development of an electrical communication network system, using the phloem tissue to transmit signals and the corresponding information over long distances within the plant body (Fromm and Lautner, 2006, 2007).

2. Types of electrical signals

Various types of electrical signals are transmitted along the phloem pathway. In general, two main types of signals occur in plants, rapid action potentials (APs) propagate with velocities of 0.5–20 cm/sec while the velocity of variation potentials (VPs) is in the range of 0.1–1.0 cm/s (Fromm and Lautner, 2007; Stahlberg and Cosgrove, 1997). Moreover, electrical signals are characterized on the basis of amplitude, duration and profile. Composite signals involving both APs and VPs can be evoked by strong damage such as burning (e.g. van Sambeek and Pickard, 1976; Hlavackova et al., 2006) when detected near the burning site (Davies and Stankovic, 2006; Hafke et al., 2009). Due to the different speeds APs and VPs drift apart with increasing distance indicating that shapes of electrical signals change along the transmission route. Composite signals often prevent correct analysis of the AP and VP constituent.

APs are generally triggered by non-invasive stimuli (Trebacz et al., 2006; Fromm and Lautner, 2006). They are transmitted along the phloem over long distances (Fromm and Eschrich, 1988) and regulate rapid leaf movements in touch-sensitive plants such as *Mimosa* (Fromm, 1991) and Venus flytrap (Hodick and Sievers, 1989; Hedrich, 2012). Furthermore, the bending of sundew leaf tentacles is also triggered by APs (Williams and Pickard, 1972a,b; Williams and Spanswick, 1976). In addition, cold-shock (Lautner et al., 2005) as well as pollination also induces APs with specific physiological functions (Fromm et al., 1995). Typical APs are spike-like changes of the resting potential with a duration of 3–300 s. As in animal neurons, APs follow the all-or-nothing principle (Fromm and Spanswick, 1993). Independent of the stimulus strength, after a critical membrane potential threshold is exceeded APs are transmitted with defined amplitudes and propagation speed. Their kinetics depend on voltage-dependent ion channels within the plasma membrane and the ionic mechanism causing an AP has a remarkable resemblance within the various plant species investigated so far (Iijima and Sibaoka, 1981; Fromm and Spanswick, 1993; Fisahn et al., 2004; Felle and Zimmermann, 2007; Lunevsky et al., 1983; Okihara et al., 1991; Homann and Thiel, 1994). In general, a stimulus-triggered opening of Ca^{2+}-channels in the plasma membrane causes a transient increase of the cytoplasmic calcium concentration correlated to an initial depolarization. The increased Ca^{2+} concentration triggers Cl^- efflux through Ca-dependent anion channels (Okihara et al., 1991; Homann and Thiel, 1994). Subsequently, voltage-dependent K^+ channels are gated causing K^+ efflux associated with a repolarization of the membrane potential.

VPs are mostly evoked by injury such as burning (Houwink, 1935; Stankovic et al., 1998; Gallé et al., 2013) or hot water treatment (van Sambeek and Pickard, 1976). They do not follow the all-or-nothing principle, are correlated to the stimulus strength and last for some seconds up to 30 min (Stahlberg et al., 2006). In addition, they have a slower transmission speed than APs and their amplitude decreases with increasing distance from the site of stimulation along their pathway (Davies, 2004; Stahlberg et al., 2006). VPs are able to pass dead tissue and are generated in the xylem after the negative hydrostatic pressure declines through damage. The ionic basis is different from that underlying APs since they are induced by a transient inhibition of proton pump activity (Stahlberg et al., 2006) and gating of mechanosensitive Ca^{2+}-channels.

3. Pathways of signal transmission

Electrical signals can propagate over short distances via plasmodesmata and electrical coupling via plasmodesmata was shown previously in various species such as *Nitella* (Spanswick and Costerton, 1967), *Elodea* and *Avena* (Spanswick, 1972). While plasmodesmata are relays in the signalling network between neighbouring cells, long distances can only be bridged rapidly via low resistance connections extending throughout the whole plant such as the elongated sieve tubes. Due to the relatively large sieve plate pores, the continuity of the plasma membrane and the saline cytoplasm (approximately 100 mM K^+) sieve tubes are optimal pathways for electrical communication between organs. In addition, a vast set of Ca^{2+}-channels occurs in the plasma membrane of the sieve elements (van Bel et al., 2014), needed for primary responses to abiotic and biotic changes. However, since the phloem is located inside the plant body electrical signals are often difficult to measure. An elegant method is the so-called aphid stylet technique in which the microelectrode tip is brought into contact with the sieve tube exsudate appearing at the cut end of an aphid stylet (Wright and Fisher, 1981; Fromm and Eschrich, 1988). By using this technique electrical signals could be measured in a variety of plant species such as *Mimosa* (Fromm, 1991), maize (Fromm and Bauer, 1994) and poplar (Lautner et al., 2005).

Interestingly, electrical signalling within the sieve tubes also affects assimilate transport. For instance, in maize leaves cold-stimulation induces APs propagating at speeds of 3–5 cm s^{-1} which cause a strong reduction of phloem transport in distant leaf parts, as shown by autoradiography (Fromm and Bauer, 1994). Since the concentrations of K^+ and Cl^- decrease in the sieve element cytoplasm after stimulation, a reduced cell turgor might be one reason for the stoppage of phloem transport. Furthermore, the reduction of phloem transport may have been caused by sieve plate occlusion with callose, which is induced by Ca^{2+}-influx during electrical signalling. Recently, it was shown that the callose concentration increased significantly in chilled maize leaves, indicating that cold-induced APs trigger callose synthesis (Fromm et al., 2013). Another mode of sieve tube occlusion is a dispersion of forisomes which turned out to be quicker than callose production (Furch et al., 2007, 2009) and is also under control of calcium (van Bel et al., 2014). Apart from APs also wound-induced VPs are transmitted in sieve tubes. However, in maize they did not inhibit phloem transport but did reduce the amount of assimilates in phloem and bundle sheath cells which might be caused by a