

## 12 Long-Distance Electrical Signaling and Physiological Functions in Higher Plants

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### 12.1 Introduction

Plants possess most of the chemistry of the neuromotoric system in animals, i.e. neurotransmitter such as acetylcholine, cellular messengers like calmodulin, cellular motors, e.g. actin and myosin, voltage-gated ion channels and sensors for touch, light, gravity and temperature. Although this nerve-like cellular equipment has not reached the same great complexity as is the case in nerves, a simple neural network has been formed within the phloem, enabling it to communicate successfully over long distances. The reason why plants have developed pathways for electrical signal transmission most probably lies in the necessity to respond rapidly to environmental stress factors. Different environmental stimuli evoke specific responses in living cells which have the capacity to transmit a signal to the responding region. In contrast to chemical signals such as hormones, electrical signals are able to rapidly transmit information over long distances. Most of the plant action potentials studied so far have a velocity in the range of  $0.01\text{--}0.2\text{ m s}^{-1}$ . However, in soybean, action potentials reached conduction rates of up to  $30\text{ m s}^{-1}$ , similar to the speed of action potentials in nerves (Volkov et al. 2000).

As regards the origin of the neuronal system in plants, it appears unlikely that it was adopted from animals. In our search for the common evolutionary roots of action potentials in plants and animals, we need to look at unicellular ancestors which do not need to transmit signals over long distances. The function of electrical transmission has most probably evolved at a later evolutionary stage. The assumption is that in the course of evolution the development of plants and animals branched off into different directions. Since cellular excitability was found to exist in primitive organisms, it is obvious that both plants and animals inherited their basic neuronal capabilities from their bacterial ancestors (Simons 1992). Szmecman and Adler (1976) observed changes in membrane potential during bacterial chemotaxis. Even the sensitivity to mechanical touch is known to be an early evolutionary achievement. Martinac et al. (1987) detected pressure-sensitive ion channels

in *Escherichia coli*, suggesting that these channels have an osmotic function. For the early evolution of action potentials, an osmotic function can also be assumed in unicellular alga such as *Acetabularia* (Mummert and Gradmann 1976). A mechanosensitive ion channel was also found in the yeast plasma membrane (Gustin et al. 1988), providing convincing evidence that plants inherited mechanical sensitivity from bacterial ancestors in the course of millions of years of evolution. The characean algae, which include *Chara* and *Nitella*, are also known to be the ancestors of higher plants. Action potentials were observed in the internodal cells of *Nitella* in 1898 by Hörmann, who used extracellular electrodes long before they were observed in isolated nerve cells by Adrian and Bronk (1928). Characean internodal cells respond to electrical stimulation in a manner similar to the contraction response displayed by skeletal muscles following electrical stimulation by nerve cells. In characean cells, electrical stimulation causes the cessation of protoplasmic streaming which is incited by the same interactions between actin and myosin that cause contraction in muscles (Hörmann 1898). In the course of evolution, once plants had gained and settled on dry land, their excitability and neuronal capability were used to develop numerous survival tactics. For instance, one important step was the development of fast-moving stomatal guard cells in response to environmental changes, while another was the electrical communication system which uses the phloem to transmit information over long distances within the plant body (Fromm and Lautner 2005).

## 12.2 Perception of electrical signals

Electrical signals can be generated at any site of the symplastic continuum by environmental stimuli such as changes in temperature, touch or wounding. Recently, it was found that acid rain also induces action potentials (Shvetsova et al. 2002), as well as irradiation at various wavelengths which induces action potentials in soybean with duration times and amplitudes of approximately 0.3 ms and 60 mV, respectively (Volkov et al. 2004). Upon perception, electrical signals can be propagated via plasmodesmata to other cells of the symplast (van Bel and Ehlers 2005). As a first step, the plasma membrane is being depolarized, a process known as formation of the receptor potential, e.g. by mechanical stimulation as observed in *Chara* (Kishimoto 1968). The receptor potential is an electrical replica of the stimulus lasting for the period of time that the stimulus is present. An action potential is evoked when the stimulus is great enough to depolarize the membrane to below a certain threshold. Subsequently, the action potential characterized by a large transient depolarization allows the rapid transmission of information via plasmodesmata (Fig. 12.1). An action potential usually has an all-or-nothing and self-amplifying character, and it travels with constant velocity and magnitude (Zawadzki et al. 1991). Electrical coupling via plasmodesmata was demonstrated in a variety of species such as *Nitella*