# 17 Electrical Signals in Plants: Facts and Hypotheses

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## 17.1 What is the context?

Electrical signals were first described over 200 years ago in both plants (Berthelon 1783) and animals (Galvani 1791), and had become an important line of study in plants over 140 years ago (Burdon-Sanderson 1873; Darwin 1875); thus they are far from being a novel phenomenon. Most of the earlier work (Burdon-Sanderson 1873; Darwin 1875), involved insect-trapping plants, which, like the sensitive plant, *Mimosa pudica*, have very rapid and visually striking responses to touch (reviewed in Simons 1981; Braam 2005) and were the preferred organisms for study for over a century. Until about 1880, there seemed to have been general acceptance of electrical signals as common to plants and animals; indeed, they were the only mechanism known for intercellular communication in any living system. However, shortly after his work on electrical signals, Darwin (1875) postulated the existence of chemical signals in plants (Darwin 1881), thus, plants were recognized as having both electrical and chemical signals, while animals had only electrical. Then, with the discovery of animal hormones and the emergence of the field of endocrinology at the turn of the (twentieth) century, it was accepted that both animals and plants had both types of signal.

Work on electrical signals in plants continued in the twentieth century, especially in India (e.g. Bose and Das, 1925), and to a lesser extent the USA (e.g. Pickard 1973), yet there seems to have been a paradigm shift, the existence of electrical signals, at least in "normal" plants was questioned. There are at least two reasons for this. First, almost concomitant with the publication of Pickard's (1973) review of action potentials in plants, there appeared a book (Tompkins and Bird 1973), aimed at the general public, which was based to a large extent on irreproducible results reported by an FBI lie detector expert (Backster 1968). This work caught the public's imagination (at least in the USA), but caused immense consternation among genuine plant scientists, since the entire field of plant electrophysiology was rendered suspect (Galston and Slayman 1979). Second, there was an underlying assumption that there was no real need for rapid signals in organisms as sluggish as

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plants. Thus, research on electrical signals in plants hit an impasse, particularly in the USA, where funding effectively stopped for 2 decades. However (and despite this lack of funding), the field has opened up again over the last 25 years, and there is increasing consensus that electrical signals in plants do, indeed, exist, not only in those with rapid movements, but in all plants. This recognition has come about at least in part from the realization that "normal" plants can have very rapid systemic responses on fundamental processes such as gene expression (Davies and Schuster 1981a,b) and this requires the generation and transmission of even more rapid systemic signals (Davies 1987a,b). This recognition of the need for electrical signals in plants is also manifested by the very recent "First Symposium in Plant Neurobiology" (see: http//izmb.de/zellbio/volkmann/index.html) and the publication of a book with articles from that Symposium (Baluska et al. 2006) as well as the publication of this present textbook, the first ever devoted to plant electrophysiology. To summarize, the main "fact" emerging from the first section is that electrical signals do, indeed, occur in most, if not all organisms (including plants), not just those exhibiting rapid and visibly-obvious responses.

## 17.2 What are major definitions and types of signal?

For the purposes of this article, a stimulus is anything that evokes a response within the plant (termed "stimulus–response coupling" in the animal literature), while a signal is anything which is generated and transmitted by the plant in response to that stimulus. Thus the stimulus might be applied from outside the plant, while the signal *must* be generated within the plant. Further, the signal itself becomes a stimulus when it arrives at its destination and provokes its own response.

As an example to expound on this point (and references will be furnished later in the appropriate sections), when voltage is applied to a plant (electrical stimulation) it can evoke the generation of an electrical signal (action potential, or AP), which is transmitted through the plant. This traveling AP almost certainly involves calcium influx into the cytoplasm followed by chloride and potassium efflux. These sub-components of the AP signal, such as increased cytosolic calcium, become stimuli when they evoke responses further downstream, such as the activation of phospholipase C. Phospholipase C can be thought of a signal in the vicinity of the plasma membrane, where it becomes a stimulus and evokes the release of inositol phosphate metabolites. These metabolic signals (especially $IP_3$), can then act as stimuli to evoke release of more calcium from intracellular stores. Finally, these signals ($IP_3$, calcium and/or their associated protein phosphorylation events) can then act as stimuli to modulate gene expression (Davies and Stankovic 2006). This sequence of

$$\text{stimulus} \rightarrow \text{signal} = \text{stimulus} \rightarrow \text{signal} = \text{stimulus} \rightarrow \text{signal}$$