9 Magnetic Measurements in Plant Electrophysiology

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9.1 Introduction

Plants show a huge range of dynamic electrical phenomena, including triggered (Umrath 1929) and autonomous action potentials (AP) (Gradmann et al. 1993), or stimulus-evoked slow transient depolarizations (Roblin and Bonnemain 1985). This electrical activity can comprise singular events (Umrath 1929), trains of periodic activity (Williams and Pickard 1972) or even long lasting periodic oscillations of the membrane voltage (Gradmann et al. 1993). Electrical activity can occur in single cells (Gradmann 1976; Bauer et al. 1997) as well as in complex plant tissues (Bentrup 1979). Many of these electrical phenomena resemble electrical activity in animal cells, and by pure analogy it has been proposed that plant cells may function like nerves, and that plants may even have the equivalent of a nervous system (Baluska et al. 2005). Irrational views like these are only possible on the background of a serious ignorance of the physics and molecular basis of electrical activity in plants. Currently we neither really understand the elementary mechanisms underlying electrical activity in plants on the same level as for example the action potential in animal cells, nor do we have clear-cut ideas on their physiological roles. In most cases also, the cellular connections and pathways that propagate electrical activity are not yet certain. Consequently, the mechanistic basis for propagation of electrical activity is also not resolved; it is still a matter of debate whether the signal is really propagated electrically like in nerves or the result of a traveling chemical wave.

The application of new experimental methods such as patch clamp technology (Okihara et al. 1991; Homann and Thiel 1994) has in the past 2 decades brought some deeper insight into the molecular basis of membrane excitation in plants. Combination of classical electrophysiology with fluorescent markers (Rhodes et al. 1996) or molecular sensors (Pena-Cortes et al. 1995) is now also paving the way to address fundamental questions on long distance propagation. A new promising method to address many of these open questions is provided by the magnetic measurements of electrical

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Plant Electrophysiology – Theory & Methods (ed. by Volkov)

activity in plants. This non-invasive method presents a tool for both high-resolution recordings on the cellular level and time resolved imaging of electrical activity over a whole plant. The present review guides through the theoretical background of the method and shows its application in a few case studies.

9.2 On SQUID sensors

A suitable method to obtain electric current is by measuring the magnetic field and calculating the current by applying Ampère's law or Biot-Savart's law. This method has in addition the advantage of being non-disturbing—what is more than non-invasive—it does not even touch the current source. The frequency of measured current is also an important parameter. High frequency currents can be easily detected even if they are very weak. On the other side, weak quasi-dc or even dc currents are not easily detected magnetically.

The promising magnetic detector of weak quasi-dc currents became operational with the development of superconducting quantum interference devices, known by the acronym SQUID. These most sensitive sensors for low frequency magnetic fields are available since early the 1970s (Zimmerman et al. 1970). Today, they have improved to the extent that we can also measure the very weak human brain signals and practically all other electrophysiological signals in living organisms.

What is the SQUID (See for instance Tinkham 1996) and how does it work? The quick answer is: SQUID is a very sensitive magnetic flux-to-voltage converter for low frequency magnetic fields. In order to get a view into the functioning of SQUID, we have to apply the rules for describing physics of the micro-world: the quantum mechanics. We need to look at three important facts in physics: superconductivity, quantum tunneling and magnetic flux quantization.

The phenomenon of superconductivity was discovered in 1911 by the Dutch physicist Heike Kamerlingh Onnes (1911). He noticed that mercury shows no electrical resistance when cooled to the temperature of liquid helium (4.2 K). Later on, several other metals and alloys were found to experience the same effect when cooled to very low temperatures. The explanation of this low temperature superconductivity [in opposition to the high temperature conductivity discovered by Karl Alex Mueller and Johannes Georg Bednorz in 1986 (Bednorz and Mueller 1986) and not yet sufficiently explained] came rather late: In 1957, John Bardeen, Leon N. Cooper and J. Robert Schrieffer published the theory (Bardeen et al. 1957) now known as the BCS theory of superconductivity. They have explained superconductivity as a result of the existence of pairs of electrons, now called Cooper pairs, each of which is formed of two electrons of opposite spin and momentum. Hence, the Cooper pair has a zero net spin and zero net momentum. Pairing of electrons is caused