18 Electrophysiology of Plant Gravitropism

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18.1 Introduction

Earth's gravitational field influences plant growth, morphology, and development. The vector of the gravity force is powerful enough to largely dominate the other directional tropic stimuli to which plants respond. Both roots and shoots respond to gravistimulation with differential, directional growth, through processes known as positive and negative gravitropism, respectively (Darwin 1896). Some of the cellular events that underlie gravitropic responses are known (recently reviewed by Morita and Tasaka 2004); the completion of a mechanistic model of plant gravity responses remains an elusive objective.

In roots, the gravity-sensing cells are the columella cells located in the root cap. These cells, known as stacocytes, contain starch-filled amyloplasts that sediment in the direction of gravity (Masson 1995). In shoots, the gravity-perceptive tissue is the endodermis, which contains sedimentable amyloplasts (Tasaka et al. 1999). In both roots and shoots, the perceived gravitropic stimulus is transduced to cells that start exhibiting differential growth, resulting in organ bending and reorientation. Little is known about the signaling pathway linking gravity perception to differential growth responses, either in the root, or in the shoot.

Plant cells exhibit a spectrum of bioelectric characteristic including electrical potentials, conductance, impedance, and permeability. Plant physiological functions are closely intertwined with cells' electric properties, through processes that involve energy maintenance and ion exchange with the environment. Steady-state electrical potentials can be measured across the plasma membrane, using microelectrodes and patch-clamping techniques. On the external plant surface, electrical potentials and ion fluxes are monitored using surface-contact electrodes and vibrating probes.

A variety of abiotic stimuli induce electrical activity in plants. The best-characterized electrical signals in plants are the action potentials and the variation potentials ("slow waves"). Voltage-gated, mechanosensitive, and ligand-activated ion channels, as well as proton pumps, are involved in

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generation and maintenance of these bioelectric potentials. Action potentials and variation potentials are both local and intercellularly propagated electrical signals. Transmitted to distant regions, these signals trigger an array of systemic molecular and cellular responses (reviewed by Davies and Stanković 2005). The information that the electrical signals carry and the responses that they evoke depend on either the ions traversing the membrane, the change in membrane potential, or both.

Despite the long-documented existence of gravity-induced electrical activity in plants, this field is marked with a surprising dearth of investigation. Discovered a century ago in the petioles of *Tropaeolum* as a differential change in extracellular electric potential (Bose 1907), the phenomenon of gravielectricity has been rarely studied by either electrophysiologists or by researchers studying gravitropism. Therefore, coming forth with a hypothesis to describe gravielectrical responses in plants is a speculative endeavor.

This review summarizes the state of knowledge related to the role of extra- and intra-cellular electrical activity in gravistimulated higher plants. The seminal studies concerning the electrophysiology of plant gravitropism are highlighted. A few ideas on the correlation of electrical activity with responses to gravity are presented. In conclusion, a prospect for future research on the electrophysiology of gravitropism is suggested.

18.2 Extracellular gravielectric potentials

The early studies on involvement of electrical potentials in plant gravitropism involved measurements of extracellular electric potentials. In the heroic age of discovery of plant electrical activity, measurements were done using extracellular, surface contact electrodes, using ionic bridges typically consisting of diluted potassium chloride. Following the studies of Bose (1907), pioneering investigations in the field were conducted by Brauner (1927), Clark (1937), and Schrank (1947). These studies provided evidence that reorientation of plants induces transient electrical activity, a phenomenon that was dubbed “geolectric effect”. Decades had to pass before that phenomenon received further attention from plant biologists.

18.2.1 Shoots

Plants are electrically active. They generate characteristic steady-state transmembrane potential differences and extracellular ionic current patterns. Bioelectricity may be involved in the establishment of plant cell and organ polarity (Nechitailo and Gordeev 2001). For example, electrical current flows along the surface of upright-growing epicotyls (Toko et al. 1989, 1990). On the physically lower end of the organ, the plasma membrane is hyperpolarized by