20 Electrophysiology and Plant Responses to Biotic Stress

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Plants respond actively to biotic stress by sensing and triggering cascades of signals that lead to the production of toxic compounds, spreading from secondary metabolites to reactive oxygen species. Here, we show that the evaluation of plasma transmembrane potential (V_m) is a powerful tool for the deciphering of earlier events following biotic attacks. After a short introduction and definition of abiotic and biotic stress, we describe how plants react to herbivore attack by changing V_m and how this can be measured using electrophysiology.

20.1 Abiotic and biotic stress

20.1.1 What is an abiotic stress?

One important feature distinguishing plants from other complex multicellular organisms is that plants are static organisms and thus cannot escape environmental challenges. Abiotic stresses are caused by physical Earth's forces such as salt, water, light, heat and cold stresses. Although clearly different from each other in their physical nature, each of them elicit specific plant responses as well as activate some common reactions in plants (Zhu 2001). Abiotic stresses, such as drought, salinity, extreme temperatures, chemical toxicity and oxidative stress are serious threats to agriculture and result in the deterioration of the environment (Wang et al. 2003). Abiotic stress is the primary cause of crop loss worldwide (more than 50% yield reduction for most major crop plants; Boyer 1982; Bray et al. 2000). Abiotic stress often leads to morphological, physiological, biochemical and molecular changes affecting plant growth and productivity (Wang et al. 2001). Abiotic stresses may activate cell signaling pathways (Knight and Knight 2001; Zhu 2001, 2002) and cellular responses (Wang et al. 2003) that can lead to alteration of the transmembrane potential (V_m). In general, V_m variations depend on unbalanced ion distribution across the plasma membrane and depolarization occurs

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when cations (such as K^+ and Ca^{2+}) are allowed to enter the cell or upon anion efflux. On the other hand, hyperpolarization mainly depends on the activity of the plasma membrane H^+-ATPase or when inward anion channels (or outward cation channels) are opened. The primary candidate for intercellular signaling in higher plants is the stimulus-induced change in V_m and excitation waves transmit information from one part of the plant to another with a speed of propagation of the action potential that in soybean can reach 40 m s^{-1} (Shevstova et al. 2001). Since ion fluxes through channels directly influence V_m, it seems reasonable to assume that molecules able to act on channel activity might be considered as important factors inducing electrical signals (Maffei et al. 2004). Under abiotic stress, the up-regulation of free radical scavenging systems is a common component of the response (Pasternak et al. 2005), as are heat stress (Dat et al. 1998; Larkindale and Knight 2002), UV-radiation stress (Brosche and Strid 2003), photoinhibition (Muller-Moule et al. 2003), heavy metal stress (Pinto et al. 2003) and anoxia (Blokhina et al. 2001). All of them may have consistent repercussions on the balance of ions across the plasma membrane, and hence on V_m. Emerging evidence suggests a broader role for common signals (such as reactive oxygen species) that mediate responses to abiotic environment, developmental cues, infection and the programmed cell death in different cell types (Torres and Dangl 2005) making tools to detect abiotic stress responses useful to quantify other plant responses. While trying to balance water deficits and carbon assimilation, plants must integrate additional information on light quality, nutrient status and temperature to make “informed decisions” to add to the pressure posed by the presence of biotic stress.

20.1.2 What is a biotic stress?

As primary producers in the food chain, plants are the source of carbon, protein, vitamins and minerals for all heterotrophic organisms, from bacteria to humans. Thus we can define biotic stress as the pressure posed on plants by living organisms. In recent years, the molecular basis of biotic stress responses in plants (Maleck et al. 2000) has been identified (reviewed by Karpinski et al. 2003). Among biotic stress, the most studied are microbial infections and herbivore attack. Based on their effects on the plant, microbes interacting with plants can be classified as pathogenic, saprophytic and beneficial. Pathogens can attack leaves, stems or roots. Current models of the mechanisms of plant defense against pathogen infection are based on animal models, and have been recently linked to the light-sensing network and to the oxygen-evolving complex in photosystem II (PSII) (Abbink et al. 2002). Much progress has been made in understanding the mechanisms by which plants detect and defend themselves against pathogens (Kunkel and Brooks 2002). Progress has been done in cloning and characterization of plant disease resistance genes that govern the recognition of specific pathogen strains