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PRIMARY MECHANISMS OF PLANT STRESS SIGNALING: AN INTERPLAY OF REACTIVE OXYGEN SPECIES, CYTOSOLIC CALCIUM AND POTASSIUM
Plenary Talking Points

Активные формы кислорода играют важные роли в физиологии растений. Они вовлечены в процессы роста, развития, регуляции биосинтезов и стрессовые ответы. Ионные каналы, которые имеют Цис.- и Гис.-содержащие центры, чувствительные к активным формам кислорода, способны воспринимать рост уровня H_2O_2, запуская эффекты входа Ca^{2+} в цитоплазму и потери клетками K^+.

Reactive oxygen species play critical roles in plant physiology. They are involved in growth, development, regulation of biosyntheses and stress responses. Ion channels, which have Cys- or His-containing ROS-sensitive moieties, can perceive increase of H_2O_2 level, triggering Ca^{2+} influx to the cytosol and loss of K^+.

Ключевые слова: активные формы кислорода; кальций; калий; ионный канал; стрессовые ответы.

Keywords: reactive oxygen species; calcium; potassium; ion channel; stress responses.

Reactive oxygen species (ROS) are critically important for plants' life. ROS are produced by intracellular and extracellular mechanisms and accumulate in the cell wall (apoplast), where the antioxidant capacity is much lower than in cytosol. The moderate generation of ROS is involved in normal plant physiology and stress responses, but their overproduction, for example during severe environmental stress or damages, results in irreversible oxidative damage and dysfunction of cell components. Major systems generating ROS in plants include electron-transporting chains in organelles, NADPH oxidases, peroxidases and some specialized oxidases. In most cases, ROS generation leads to elevation of cytosolic free Ca^{2+}, the major second messenger in plant cells, transducing redox signals into genomic, metabolic or ion transport/cargo responses. This reaction relies on the presence of ROS-activated Ca^{2+}-permeable cation channels in the plasma membrane of higher plants. On the other hand, NADPH oxidases (enzymes producing ROS extracellularly) include the cytosolic EF-hand Ca^{2+}-binding motif, which is directly controlled by Ca^{2+} level in the cytosol. Overall, ROS sensitivity of Ca^{2+} influx systems and Ca^{2+} regulation of ROS production allow to propose a ROS-Ca^{2+} hub for generation and amplification of environmental stimuli . The question of sensing ROS by ROS-activated ion channels is still debated in plant physiology. Here, it is demonstrated that the plasma membrane ion channels transporting cations, such as Ca^{2+} and K^+, may have specific His-containing moieties in their structure, which are prime targets of extracellular ROS. These systems can catalyse early and rapid sensing of ROS in plants involved in a multitude of physiological reactions, such as adaptation to stresses, control of photosynthesis, cell elongation and gravitropic responses. In the plasma membranes of lower and higher plants, ROS instantaneously activate two major classes of ion channels: Ca^{2+}-permeable nonselective cation channels (NSCCs) and K^+ outwardly-rectifying channels (KORs encoded by GORK). Activation of cation channels by ROS leads to dramatic influx of Ca^{2+} for signaling, developmental and nutritional needs and K^+ loss (electrolyte leakage) inducing autophagic and necrotic cell death. Ca^{2+} entry also rearranges actin cytoskeleton and modifies vesicular transport. ROS-activated ion channels reveal complex nature of activation, depending on the developmental stage and oxidative capacity of tested ROS. The transition metal binding centres have recently been identified in some members of cyclic nucleotide-gated channels, a subclass of NSCCs. These centers potentially produce hydroxyl radicals from H_2O_2 (Haber-Weiss reaction) directly in the channel's macromolecule. Mutations in ROS-sensitive moieties in K^+ efflux GORK channel leads to the decrease of ROS-sensing capacity, suggesting that distinct molecular groups are responsible for ROS sensing by ion channels. These moieties probably confer physiological properties related to ROS, such as programmed cell death and autophagy.