



Research review paper

Improvement of stress tolerance in plants by genetic manipulation of mitogen-activated protein kinases

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ABSTRACT

Plant stress tolerance depends on many factors among which signaling by mitogen-activated protein-kinase (MAPK) modules plays a crucial role. Reversible phosphorylation of MAPKs, their upstream activators and downstream targets such as transcription factors can trigger a myriad of transcriptomic, cellular and physiological responses. Genetic manipulation of abundance and/or activity of some of these modular MAPK components can lead to better stress tolerance in *Arabidopsis* and crop plant species such as tobacco and cereals. The main focus of this review is devoted to the MAPK-related signaling components which show the most promising biotechnological potential. Additionally, recent studies identified MAPK components to be involved both in plant development as well as in stress responses, suggesting that these processes are tightly linked in plants.

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Abbreviations: ABA, abscisic acid; ACC, 1-amino-cyclopropane-1-carboxylic acid; ACS6, ACC synthase 6; BAK1, BR1-associated kinase 1; CTR1, constitutive triple response 1; EF-Tu, elongation factor thermo-unstable; ETI, effector-triggered immunity; ETR1, ethylene response 1; FLS2, flagellin sensitive 2; FRK1, flg22-induced receptor kinase 1; HR, hypersensitive response; IBR5, indole-3-butyric acid response 5; JA, jasmonic acid; MAPK, mitogen-activated protein-kinase; MAPKK/MAP2K, mitogen-activated protein-kinase kinase; MAPKKK/MAP3K, mitogen-activated protein-kinase kinase kinase; MKP2, MAPK phosphatase 2; NLP, Nep1-like protein; NO, nitric oxide; PAD2/3, phytoalexin deficient 2/3; PAMPs, pathogen-associated molecular patterns; PCD, programmed cell death; PR, pathogenesis related; PRRs, transmembrane pattern recognition receptors; PTL, PAMP-triggered immunity; ROS, reactive oxygen species; SA, salicylic acid; SIMK, stress-induced MAPK; TMV, tobacco mosaic virus; VIP1, VirE1-interacting protein 1; Y2H, yeast two-hybrid.

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1. Introduction

Plants are sessile organisms which are constantly exposed to a variety of biotic and abiotic stresses in their external environment. In order to survive, plants developed mechanisms for rapid sensing of signals from a changing environment and for transmitting these in specific adaptive/defensive responses. In all eukaryotes, mitogen activated protein kinase (MAPK) pathways play an essential role in signal transduction involved in the regulation of growth, differentiation, proliferation, death and stress responses.

MAPK signaling pathways are regularly assembled into modules which are composed of MAPK kinase kinase (MAPKKK, MAP3K or MEKK), MAPK kinase (MAPKK, MAP2K or MEK) and MAPK. Individual members of these modules are activated by reversible phosphorylation (Fig. 1). They are believed to be held together in protein complexes with the help of scaffold proteins. These scaffold proteins along with specific subcellular localization/compartimentalization of scaffolded complexes (e.g. on endomembranes and vesicular compartments) and their individual constituents (e.g. individual MAPKs released from the complex and relocated to the nucleus) might bring certain specificity to the various signaling pathways and perhaps also avoid cross-talk with other signaling pathways. Quite often activated MAPK relocates to the nucleus and regulates transcription factors and/or other proteins involved in transcription with a main consequence of gene expression modulation and reprogramming of plant developmental program and/or stress response. Except for the nuclear proteins, however, plant MAPKs can also regulate proteins involved in cytoskeletal remodeling as well as a large number of cytoplasmic proteins (Fig. 1). Taking into account a broad spectrum of triggers and physiological outcomes plant MAPK modules emerged

as important regulators of gene expression, plant cytokinesis and development as well as ethylene and camalexin biosynthesis during the last decade. Some molecular substrates of MAPK modules such as transcription factors as well as individual members of these modules are considered as good targets for biotechnological applications. Various tools for in silico database searches including full genome transcriptomic analyses and gene expression correlation studies are available today to disentangle the complex architecture of organization of the MAPK signaling modules. This review summarizes the roles of MAPK signaling pathways with a main focus on biotic and abiotic stress, and especially on MAPK components and their molecular targets showing a biotechnological potential.

2. Short overview of abiotic stress factors triggering MAPK activity

MAPK pathways are known to be activated by diverse abiotic stresses such as cold, salt, heat, drought, wounding, UV irradiation, osmotic shock, ozone or heavy metal intoxication. The main *Arabidopsis* MAPKs activated by salt, cold, drought, touch and wounding are MPK4 and MPK6 (Ichimura et al., 2000; Teige et al., 2004). For cold and salt stresses, one complete MAPK signal transduction module was identified in *Arabidopsis*. This module consists of the MEKK1 as an upstream activator of MKK2 and the downstream MAPKs MPK4 and MPK6 (Teige et al., 2004). Additionally, also MKK1 is activated by salt, drought and wounding stress and can phosphorylate MPK4, thus it might also be involved in abiotic stress signaling (Teige et al., 2004; Xing et al., 2007). Hypoosmolarity was shown to activate MPK3, MPK4 and MPK6 in cell suspensions and plantlets of *Arabidopsis* (Droillard et al., 2004).

Ozone, as a major pollutant and potent reactive oxygen species (ROS) generator, activated MAPK signaling pathways through triggering ROS production and accumulation of ethylene, jasmonic acid (JA) and salicylic acid (SA) resulting in local programmed cell death (PCD). Ozone activated MPK3 and MPK6 and it caused the nuclear translocation of these MAPKs in *Arabidopsis* (Ahlfors et al., 2004). Such activation is independent of ethylene and JA, but activity of MPK3 is dependent on salicylic acid. Later, it was shown that MKP2 (MAPK phosphatase 2) is an important positive regulator of the cellular response to ozone since it can affect the activation state of MPK3 and MPK6 (Lee and Ellis, 2007). Suppression of MKP2 creates hypersensitivity to ozone with prolonged activation of MPK3 and MPK6. Also in tobacco, NtMPK4 plays an important role in ozone sensitivity and JA signaling. Using transgenic plants it was shown that NtMPK4 played a main role in the response to wounding, and was also involved in ozone tolerance by regulating stomatal closure (Gomi et al., 2005). Oxidative stress induced by exogenous H₂O₂ can also activate MPK1 and MPK2 (Ortiz-Masia et al., 2007), MPK3 and MPK6 (Kovtun et al., 2000), MPK4 (Nakagami et al., 2006) and MPK7 (Doczi et al., 2007) in *Arabidopsis* suggesting that ROS act upstream of several MAPK cascades.

In higher plants, MAPKs can be activated also by toxic levels of heavy metals. Cadmium and copper treatment induced *OsMAPK3* and *OsMPK6* in rice (Yeh et al., 2007). This result implies that a MAPK cascade may function in cadmium and copper signaling pathway in rice. Additionally, an activation of four distinct MAPKs such as SIMK, MMK2, MMK3 and SAMK was observed after exposure of *Medicago sativa* seedlings to the excess of copper or cadmium ions (Jonak et al., 2004). Nevertheless, distinct MAPK pathways seemed to be involved in the response to copper and cadmium stress.

Thus MAPK signaling pathways appear as universal transducers of diverse abiotic stresses in plants (Table 1).

3. Short overview of biotic stress factors inducing MAPK activity

During evolution, higher plants developed an innate immune system (Jones and Dangl, 2006) to detect pathogen attacks and to activate rapid multistep defense responses, such as the production of

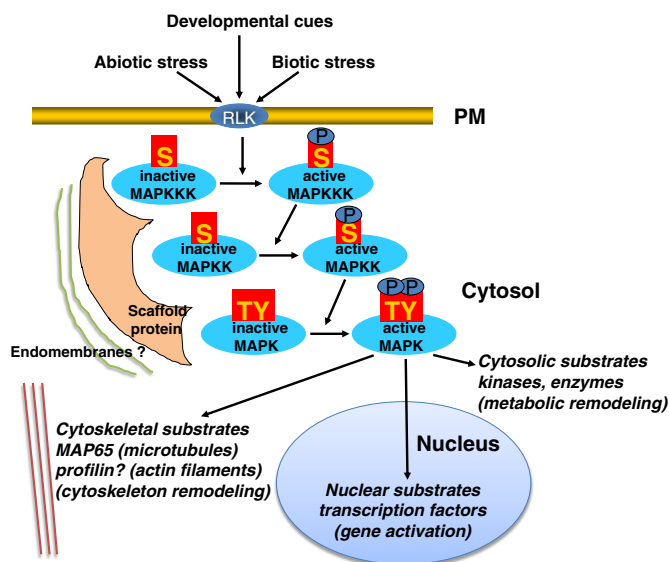


Fig. 1. Model depicting the subcellular organization of mitogen-activated protein kinase (MAPK) modules and their targets. MAPKs are phosphorylating enzymes representing main signal transducers in plants. They are organized in protein complexes, so called MAPK modules, which are held together by scaffold protein. These scaffold proteins have binding sites for MAP3K, MAP2K and MAPK and usually possess specific PH and/or FYVE domains which can bind to phospholipids in endomembranes. Eventually, also some MAP3Ks and MAP2Ks may also function as scaffold proteins. MAPK signaling can be triggered by diverse stimuli such as stress and developmental cues. During signal transduction, MAP3Ks and MAP2Ks are stepwise phosphorylated and activated on serine (S) or threonine (T) residues while MAPKs must be double phosphorylated on both threonine (T) and tyrosine (Y) residues. Activated MAPKs are released from MAPK modules, they relocate within the cell and regulate broad range of substrates (e.g. transcription factors, protein kinases, enzymes and cytoskeletal proteins) which are localized in/at diverse subcellular compartments (nucleus, cytosol, cytoskeleton). This subcellular compartmentalization of MAPK modules (e.g. association with endomembranes or with cytosol) and targets of activated MAPKs (e.g. nucleus, cytosol, cytoskeleton) is believed to bring some specificity to the MAPK signaling.

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