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Plant MAPK cascades: Just rapid signaling modules?

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Abscisic acid (ABA) is a major phytohormone mediating important stress-related processes. We recently unveiled an ABA-activated MAPK signaling module constituted of MAP3K17/18-MKK3-MPK1/2/7/14. Unlike classical rapid MAPK activation, we showed that the activation of the new MAPK module is delayed and relies on the MAP3K protein synthesis. In this addendum, we discuss the role of this original and unexpected activation mechanism of MAPK cascades which suggests that MAPKs can regulate both early and long-term plant stress responses.

Keywords: Abscisic acid, ABA signaling, delayed signaling, mitogen-activated protein kinase, protein synthesis

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Mitogen Activated Protein Kinase (MAPK) modules are minimally constituted of 3 kinases, a MAP3K (for MAP2K Kinase), a MAP2K (for MAPK Kinase) and a MAPK. These kinases sequentially activate each other by phosphorylation to mediate signaling from receptors to downstream effectors in the appropriate compartments.[1,2] In plants, extensive functional studies of 3 stress-activated MAPKs – MPK3, MPK4 and MPK6 – have led to the model that MAPK modules are early signaling actors which modulate a first wave of rapid and non-specific cellular responses. For example, upon treatment with PAMPs (pathogen-associated molecular patterns) that are detected by several plant receptors to activate PAMP-Triggered Immunity (PTI), MAPK activities increase within 5 minutes, peak at 15 minutes and return to basal levels by 60 minutes.[3-5] Consequently, kinases belonging to these MAPK modules have to be expressed even in non-stress conditions, when the signaling module is inactive. This has been experimentally confirmed for MPK3, MPK4 and MPK6 using specific antibodies.[6] More generally, genes coding for stress-related MAPK modules were shown to be only weakly modulated by stresses.

We recently unveiled MAP3K17/18-MKK3-MPK1/2/7/14 as a new complete MAPK module that is activated by abscisic acid (ABA) in an ABA-core-signaling-module-dependent way.[7] Surprisingly, the kinetics of MPK7 activation is slower than expected for an early stress-responsive pathway as it occurs only hours after ABA treatment. Moreover, *MAP3K17* and *MAP3K18* transcripts are barely detectable in resting conditions but strongly accumulate after ABA treatment. Using transgenic lines expressing a tagged version of MAP3K18 under the control of its own promoter in the *map3k17/18* mutant background (*map3k17/18-MAP3K18locus-YFP*), we showed that MAPK3K18 protein abundance largely follows MAP3K18 transcript levels which only accumulate after ABA treatment (**Fig. 1**). In this system, the limiting step for the proper module signaling is therefore the presence of the upstream MAP3Ks which tightly correlates with the ABA-dependent MAPK activation. As a result, blocking MAP3K18 production by using the inhibitor of protein synthesis cycloheximide prevents the MAPK activation by ABA.[7] To our knowledge, this is the first time that such MAPK regulation is described in plants and animals. This finding does not exclude the possibility that MAP3K17/18 additionally need an upstream direct activator to be able to

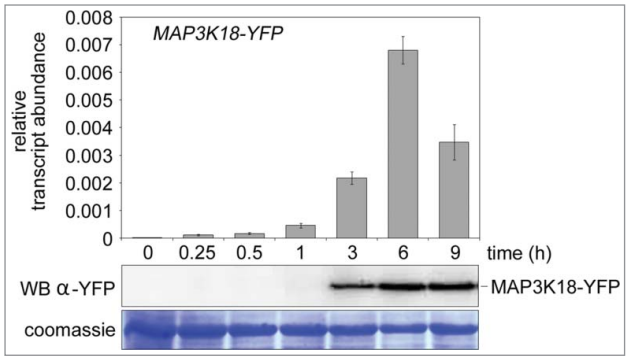

Figure 1. MAP3K18 accumulation in response to ABA at the transcript and protein levels. Seven-day-old seedlings of *map3k17/18-MAP3K18locus-YFP* were treated with 100 μM ABA for the indicated time. *MAP3K18-YFP* mRNA levels were monitored by qRT-PCR relatively to *ACTIN2* used as a reference (upper panel). MAP3K18-YFP protein levels were monitored by Western blot using anti-GFP antibody (lower panel). The membrane was stained with coomassie blue for loading control.

phosphorylate MKK3. Interestingly, a faster activation has been reported for MPK1/2 in response to ABA.[8,9] One explanation could be that in the experimental conditions used in these studies, MAP3Ks are already expressed and the module is activated independently of transcriptional regulation. This also suggests that the MAPK module could have 2 functioning modes depending on environmental conditions, which remain to be identified.

What could be the role of the delay in MAPK module activation? The consequence of such protein synthesis-dependent activation of MAP3K17/18-MKK3-MPK1/2/7/14 is that this module does not probably regulate early drought-dependent responses but is rather involved in the modulation of long-term responses. Coherently, in the *mkk3* and *map3k17/18* mutants, we did not observe any changes in ABA-induced stomatal closure, which occurs in less than half of an hour. Besides this fast physical response, ABA and drought perception also trigger plant adaptation as revealed by a large reprogramming of genome expression, including cell wall and metabolic changes as well as the modification of the plant water status.[10] Stress perception also induces chromatin marks as plant stress memory, allowing a faster and more efficient response to a second episode of drought stress.[11] The newly identified ABA-activated MAPK module may be involved in such long-term adaptation. Further studies are required to answer this question.

With the characterization of the MAP3K17/18-MKK3-MPK1/2/7/14 module, our work identified a new mechanism to activate MAPK cascades in plants through protein biosynthesis. Further studies will be necessary to clarify if this mechanism is shared by other MAPK modules or if it is specific to ABA. Interestingly, MPK3 and MPK6 displayed a delayed and sustained activation by the avirulent protein AvrRpt2 during effector-triggered immunity (ETI).[12] Although the effector injection into the plant cell may account for the delay, an exciting hypothesis could be that MPK3/MPK6 activation during ETI also depends on the biosynthesis of a MAP3K. Detailed analyses of ETI-related transcriptomic data may help to identify *MAP3K* candidate genes having such a role.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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