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RESEARCH HIGHLIGHT

Fertility control: the role of magnesium transporters in pollen development

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Magnesium (Mg^{2+}) is essential for many plant processes. It is particularly important for photosynthesis, where it is the central element of the chlorophyll molecules. Magnesium is also a constituent of many enzymes and serves as an activator of others, including DNA polymerases, protein kinases, and phosphatases. Intracellular Mg^{2+} concentration is precisely controlled by Mg^{2+} uptake, translocation across intracellular membranes and efflux [1]. Surprisingly, however, the molecular mechanisms underlying these processes in higher plants are still largely unknown. Recently, two reports [2, 3] disclosed functions of two Mg^{2+} transporters in pollen development. Pollen grains are the male gametes in flowering plants.

Mg^{2+} transporters of the CorA family appear to be the primary transport systems mediating both influx and efflux of Mg^{2+}. CorA-type transporters are widely distributed in bacteria, fungi, animals and in plants (see below). The crystal structure of the CorA transporter from the bacterium *Thermotoga maritima* has recently been elucidated revealing a unique structure with a large, acidic N-terminal domain and two transmembrane domains in the C-terminal region [4]. The currently best studied eukaryotic homologues are those from budding yeast (*Saccharomyces cerevisiae*), where the MRS2 and LPE10 proteins are targeted towards the inner mitochondrial membrane, while ALR1, ALR2 and MNR2 transporters are located in the plasma membrane [5].

Higher plant transporters of the CorA/MRS2 family were first identified in 2000, when Schock *et al*. [6] reported a gene family of ten members in *Arabidopsis thaliana*, named *AtMRS2-1* to *AtMRS2-10*. These authors also demonstrated that *AtMRS2-1* functionally complements *Mrs2*-deficient yeast restoring intramitochondrial Mg^{2+} concentration to the wild-type level.

Functional evidence for Mg^{2+} transport was also provided by Li *et al.* [7] who in 2001 discovered the same gene family, but named it as *AtMGT* (for *Arabidopsis thaliana* magnesium transporter). Most members of the *AtMGT* gene family were shown by RT-PCR to be expressed throughout the plant, with the exception of *AtMGT5* which was only expressed in flowers, and *AtMGT8* that was not expressed in stem tissue. *AtMGT1* functionally complemented a bacterial (*Salmonella typhimurium*) mutant called MM281 that lacks three Mg^{2+} transport systems (CorA, MgtA and MgtB). AtMGT1 turned out to be a high-affinity transporter for Mg^{2+}. Among divalent cations it was highly selective for Mg^{2+}. *AtMGT10* complemented a yeast mutant, lacking both *ALR1* and *ALR2* genes [7], although it localizes to the chloroplast envelope membrane when expressed in plant cells, indicating a role in Mg^{2+} uptake and translocation into chloroplasts [8]. Recently the first low-affinity Mg^{2+} transporter, AtMGT7a, was identified in higher plants. Two different transcripts are produced from the *AtMGT7* gene; *AtMGT7a* transcript is expressed in all tissues analyzed, whereas the slightly shorter *AtMGT7b* transcript is present in roots and flowers [9]. Only *AtMGT7a* complemented the *Salmonella* MM281 mutant, whereas *AtMGT7b*, which encodes a protein lacking a 15-amino acid region, did not.

The biological roles of all above mentioned Mg^{2+} transporters are still unknown although ectopic expression of *AtMGT1* in *Nicotiana benthamiana* conferred improved tolerance to aluminum [10]. However, a physiological function was recently discovered for AtMGT5 which represents a dual-functional Mg^{2+} transporter that mediates uptake and efflux of Mg^{2+} in a concentration-dependent manner when expressed in the MM281 strain [2]. At low (i.e., micromolar) concentration of Mg^{2+} the AtMGT5 protein serves as an importer, whereas at high (millimolar) Mg^{2+} levels it facilitates efflux of the divalent cation. Expression of AtMGT5-GFP fusion protein in transgenic *Arabidopsis* plants labeled mitochondria (verified by MitoTracker Red CMXRos staining), suggesting that it shuttles Mg^{2+} be-

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tween the mitochondrial compartment and the cytoplasm. Promoter-reporter (β-glucuronidase) fusion studies revealed exclusive expression of *AtMGT5* in anthers at earlier stages of flower development, in both gametophytic and sporophytic tissues [2]. Interestingly, when *AtMGT5* was mutated by T-DNA insertion, pollen formation was strongly impaired in hemizygous mutants; homozygous *atmgt5* mutants were never obtained, indicating lethality of a complete knock-out of the *AtMGT5* gene.

The story became even more fascinating when Chen *et al.* [3] described a second Mg^{2+} transporter, AtMGT9, which also affected pollen viability. AtMGT9 supported the growth of the bacterial MM281 mutant at 500 μM Mg^{2+}, but not at 10 μM Mg^{2+}, reminiscent of a low-affinity transporter. Tracer inhibition studies, that utilize the fact that Mg^{2+} and Ni^{2+} can be transported by the same CorA-type transporters with similar kinetics, revealed that AtMGT9 is able to transport Mg^{2+} at physiological concentrations normally found in plant cells, whereas the transport of other divalent ions – trace elements – appeared unlikely due to their much lower levels prevalent in plants. Transcriptional activity of *AtMGT9* in anthers followed a distinct temporal and spatial pattern. Its expression was evenly distributed throughout the anther early in development and was then concentrated in the tapetum, the tissue nursing pollens during their formation. *AtMGT9* expression vanished when the tapetum was degraded and resumed again during pollen maturation. As with *AtMGT5*, disruption of *AtMGT9* led to pollen abortion, and only hemizygous mutants survived. Crossing experiments proved that the mutated *atmgt9* allele could not be transmitted through the pollen due to lack of fertility [3].

The works by Luan and co-workers [2, 3] show a tight connection between Mg^{2+} transporter function and pollen development for the first time, although we do not know in detail how the two transporters sustain pollen formation and thus fertility. One model supposes that both proteins are located in mitochondria (though the localization of AtMGT9 still has to be investigated) but function independently to contribute to mitochondrial Mg^{2+} homeostasis. Alternatively, both proteins may constitute subunits of a hetero-oligomeric transporter. However, as both AtMGT5 and AtMGT9 seemingly form functional transporters when individually expressed in bacterial cells, it appears likely that functional (homo-oligomeric) transporters can also form *in planta*. Another scenario is that AtMGT9 resides in a non-mitochondrial membrane to exert its transport function jointly with mitochondrial AtMGT5. None of these models can be excluded at present.

A further interesting asset comes from the fact that both magnesium transporter genes follow distinct, partially overlapping tempo-spatial activity patterns during anther development. Identifying the transcription factors that govern their expression will contribute to our understanding of the regulatory networks that control pollen viability through the function of AtMGT5 and AtMGT9 transporters.

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