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A member of a new plant gene family encoding a meprin and TRAF homology (MATH) domain-containing protein is involved in restriction of long distance movement of plant viruses

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Restriction of long distance movement of several potyviruses in *Arabidopsis thaliana* is controlled by at least three dominant restricted TEV movement (RTM) genes, named *RTM1*, *RTM2* and *RTM3* and acts as a non conventional resistance. *RTM1* encodes a protein belonging to the jacalin family and *RTM2* encodes a protein which has similarities to small heat shock proteins. The recent cloning of *RTM3* which encodes a protein belonging to an unknown protein family of 29 members which has a meprin and TRAF homology (MATH) domain in its N-terminal region and a coiled-coil (CC) domain at its C-terminal end is an important breakthrough for a better understanding of this resistance process. Not only the third gene involved in this resistance has been identified and has allowed revealing a new gene family in plant but the discovery that the *RTM3* protein interacts directly with *RTM1* strongly suggests that the RTM proteins form a multimeric complex. However, these data also highlight striking similarities of the RTM resistance with the well known R-gene mediated resistance.

The RTM Resistance is not a Conventional Resistance

The resistances which control the systemic invasion of plants by viruses, even if they are widely used in crops, are poorly understood. The RTM (for Restricted Tobacco etch virus (TEV) Movement) resistance which restricts the long distance movement of some viruses belonging to

the *Potyvirus* genus (the most important plant virus genus) in *Arabidopsis thaliana* (Columbia accession), is the best studied.

This resistance does not correspond to any of the known resistance mechanisms as the R gene-mediated resistance¹ or the RNA interference.² Indeed, viral replication and cell-to-cell movement in inoculated leaves appear unaffected, HR and systemic acquired resistance are not triggered, salicylic acid is not involved.³⁻⁵ We also showed that this resistance mechanism is independent of the RNA interference as the single, double or triple RNaseIII dicer-like knockout mutants in which the RNA silencing-based antiviral response is suppressed⁶ are still resistant to potyviruses (Revers, unpublished). In addition to be active against TEV,⁷ this resistance was also showed to be active against two other unrelated potyviruses, *Lettuce mosaic virus* (LMV) and *Plum pox virus* (PPV),⁵ showing that the *RTM* genes seem to be associated to a general resistance mechanism against potyviruses. At least three RTM genes, named *RTM1*, *RTM2* and *RTM3*, are involved in this resistance process^{4,7} and seem to act in an interdependent way as a mutation in anyone of these three genes is sufficient to completely abolish the restriction of long distance movement.⁷ *RTM1* and *RTM2* were cloned at the end of the nineties and encode a protein belonging to the jacalin family⁸ and a protein which contains a transmembrane domain and a small heat shock protein domain,⁹ respectively. Both genes are specifically expressed in phloem-associated tissues.¹⁰ Recently from the

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analysis of some LMV or PPV isolates able and unable to overcome the RTM resistance, it was showed that the N-terminal domain of the coat protein (CP) is the RTM resistance-breaking determinant,¹¹ which is not surprising as this domain is involved in the potyvirus long distance movement process.¹²

***RTM3* Belongs to an Undescribed Gene Family**

The recent cloning of *RTM3* has revealed the involvement of a new gene family in the RTM resistance mechanism characterized by the presence in the corresponding protein of a meprin and TRAF homology (MATH) domain in the N-terminal part and a coiled coil domain in the C-terminal part.¹³ Interestingly, twenty-eight genes were found to contain in the corresponding protein these two domains which share for most of them more than 50% of identity with the *RTM3* domains.¹³ Sixteen of these genes are located in a cluster with *RTM3* in which five genes for which the corresponding protein contain only a coiled coil domain are also identified. Other smaller clusters of genes associating *RTM3* homologous genes with or without a MATH domain in the corresponding protein were also found in the Arabidopsis genome suggesting the role of duplication events in shaping the evolutionary history of this gene family, including the possibility of deletion or duplication of one or the other domain. The role of *RTM3* in a resistance mechanism is the first biological function identified for this gene family in plant. This is also the first function identified among the 71 Arabidopsis genes encoding a MATH protein.

It is quite surprising that any functional data are available for this gene family. As numerous MATH proteins are found in plants (Medicago, rice), in lower eukaryota (Trypanosoma, Plasmodium) and in lower metazoa such as the nematode *C. elegans*, we can assume they play important roles in cells. MATH domains seem to be important for protein-protein interaction and several studies on human and *C. elegans* MATH proteins seem to indicate they might have important functions in the regulation of protein processing.¹⁴

The Hypothesis of the RTM Protein Complex

Another major data we recently produced for the understanding of this resistance is the fact that *RTM3* directly interacts with itself and with *RTM1* in planta.¹³ This interaction suggests that the RTM proteins might act as a multiprotein complex to block the long distance movement of potyviruses. However no direct interaction has been shown between *RTM1* or *RTM3* with *RTM2* and between the RTM proteins and the CP of potyviruses. As the protein-protein interaction experiments used in this study do not allow to reveal interactions between more than two proteins, it can not rule out the possibility that the RTM complex formed by monomers of *RTM1* and *RTM3* may interact with virions or viral ribonucleoprotein complexes by the N-terminal domains of the CP monomers exposed at the surface of the virus particles.

As the RTM proteins are expressed in companion cells (CC), several mechanisms can be suggested from all these data. (1) The RTM protein complex could sequester or degrade virions or mobile viral RNPs which could not be translocated from CCs to sieve elements (SE) through plasmodesmata (PD); (2) The RTM complex could sequester one or several factors necessary for translocation of the virions/viral RNPs from CC to SE; (3) The RTM factors may induce or activate an antiviral response in the phloem tissue which recognizes and targets either the virus movement competent form through an interaction with the N-terminal end of the CP, or this N-terminal end of the CP itself from free CP monomers which might be considered as an effector. Overbreaking virus isolates which have mutation in the N-terminal domain of the CP and are therefore able to move systemically, do not interact with the RTM complex in the proposed mechanisms (1) and (3) or might be able to use other plant factors to move systemically in the case of mechanism (2).

Several arguments might be in favour of an induced plant defence response. Indeed, the identification of *RTM3* reveals intriguing and striking similarities with the dominant R-gene response in plants: (1) clustered arrays of *RTM3*, a dominant

resistance gene, and its homologs in the Arabidopsis genome showing evidence of gene duplication and deletion events; (2) *RTM3* being a protein with a CC domain that is important for the resistance response; (3) the potyvirus CP being the necessary determinant (effector?) and the indication that the recognition of this viral factor might involve a RTM multiprotein complex; (4) involvement of a heat shock protein (*RTM2*). However, there is no HR, production of SA or induction of SAR. Nevertheless as R gene-effector interactions have to date only been studied in leaf mesophyll and epidermal cells and has not been investigated in phloem-associated tissues, signalling may be different as an HR in the phloem would likely prove fatal to the plant. The RTM resistance may be a novel form of immunity.

If the cloning of *RTM3* and the characterisation of protein-protein interactions between the RTM proteins help to a better knowledge of the involved factors and their putative roles in this resistance process, it remains several important questions to solve in order to decipher this resistance mechanism. Among them, subcellular localisation of the different RTM proteins will have to be elucidated as well as the subcellular blocking of the virions/viral RNPs. The identification of the plant factors interacting either with the RTM complex and/or with virions or viral RNPs will be also an important challenge for the next years.

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