

Plant MLO proteins: Conserved "disease susceptibility factors" for powdery mildew fungi

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Powdery mildew is a widespread plant disease of temperate climates that is caused by ascomycete fungi of the order Erysiphales. The disease is macroscopically characterized by “powdery” fungal reproduction structures on the surface of plant organs (Fig. 1a). It is an important threat for both agri- and horticulture and can cause significant harvest losses in cereals and crop plants such as wheat, barley, and tomato, and severely impact ornamental plants such as roses. Accordingly, the generation of plant breeds that exhibit robust immunity to this disease is of great economic interest. One major step in this direction was the discovery of barley mutant plants that display near complete resistance to the barley powdery mildew pathogen, *Blumeria graminis* f.sp. *hordei* (*Bgh*). These plants, which carry recessively inherited loss-of-function mutations in the gene *Mildew resistance locus o* (*Mlo*), show durable broad-spectrum resistance against virtually all *Bgh* isolates. On *mlo* mutant plants, powdery mildew pathogenesis is terminated at the stage of cell wall penetration and host cell entry; consequently, fungal sporelings do not form haustoria inside host cells and fungal colonies cannot develop. Subsequent studies revealed that (1) *Mlo* genes are restricted to plants and green algae and represented as small to medium-sized families in higher plant species and (2) that *mlo*-based powdery mildew resistance is not restricted to the monocot barley, but also found in the distantly related eudicot plant species *Arabidopsis thaliana*. Mutant alleles of *Arabidopsis thaliana* *AtMLO2*, one out of the 15 *MLO* genes present in the *Arabidopsis* genome, confers partial resistance to the adapted powdery mildew species *Golovinomyces orontii* and *G. cichoracearum* (Fig. 1).

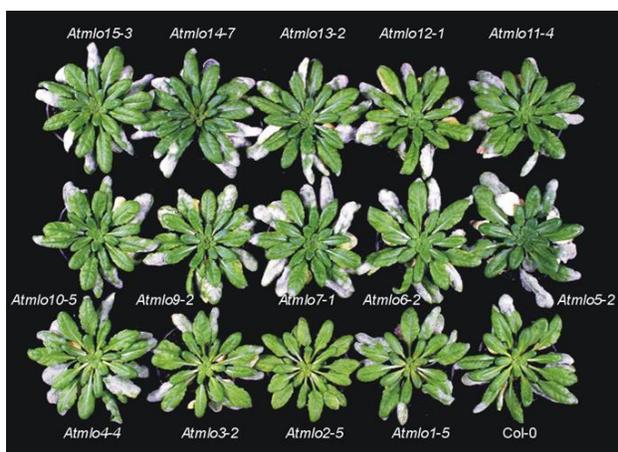


Fig. 1. Identification of the *AtMLO2* T-DNA insertion line as being resistant against powdery mildew infection.

Moreover, the triple mutant *Atmlo2 Atmlo6 Atmlo12* is completely resistant to these pathogens, restricting fungal development at the host cell entry level. These discoveries, together with the knowledge that the *MLO* family is ubiquitously present in higher plant species, led to the identification of powdery mildew resistance on the basis of natural *mlo* loss-of-function alleles in tomato and pea (Fig. 2). Conservation of *mlo* resistance across monocot and dicot plant species implicates a common mechanistic basis for this type of plant immunity. It further implies potential application of this trait for plant breeding of many other agriculturally and economically important plant species.

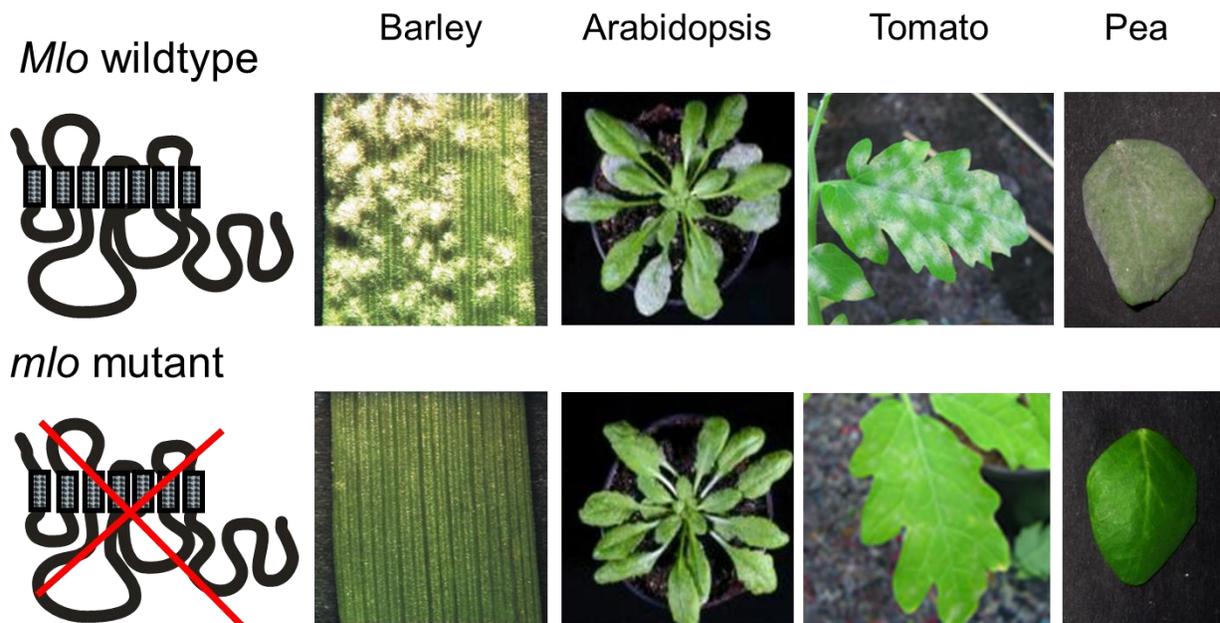


Fig. 2. Conservation of *mlo* resistance across plant species.

The broad-spectrum, non-race specific *mlo*-mediated powdery mildew resistance in barley is an excellent example for a gene that has been widely used in plant breeding and agriculture. Since more than 30 years natural and induced *mlo* alleles have granted stable powdery mildew resistance in the field. Nevertheless, the usage of plants carrying *mlo* alleles is associated with certain limitations. First, in the absence of pathogens, barley *mlo* plants spontaneously form callose-containing cell wall appositions (papillae), predominantly in the short cell type of the leaf epidermis. Additionally, leaf mesophyll cells in *mlo* mutants undergo spontaneous mesophyll cell death, which has been recognized as an indication of accelerated leaf senescence. Second, barley *mlo* alleles show enhanced susceptibility to the hemibiotrophic fungus *Magnaporthe*

oryzae and higher sensitivity to necrosis-inducing toxin from *Bipolaris sorokiniana*. Furthermore, *mlo* mutations seem to have an environment-dependent effect on the leaf spot disease caused by the necrotrophic ascomycete *Ramularia collo-cygni*. The enhanced susceptibility to certain hemibiotrophic or necrotrophic plant pathogens might be a direct consequence of deregulated cell death in *mlo* plants. These *mlo*-associated pleiotropic effects result in a reduction in grain yield, a penalty that nevertheless seems to be overcompensated by the benefit of reduced powdery mildew infection. Notably, not only the powdery mildew resistance trait but also some of the undesired side effects are phenocopied by *Atmlo2* mutant plants.

We hypothesize that the strong resistance of *mlo* mutants is either based on perturbed MAMP responses or is brought about by defence suppression by powdery mildew fungi. In the latter scenario MLO proteins might be targeted by fungal effector proteins to suppress secretion-based defence pathways that are known to be effective against non-adapted powdery mildew fungi and comprise proteins PEN1, PEN2 and PEN3 (Fig. 3).

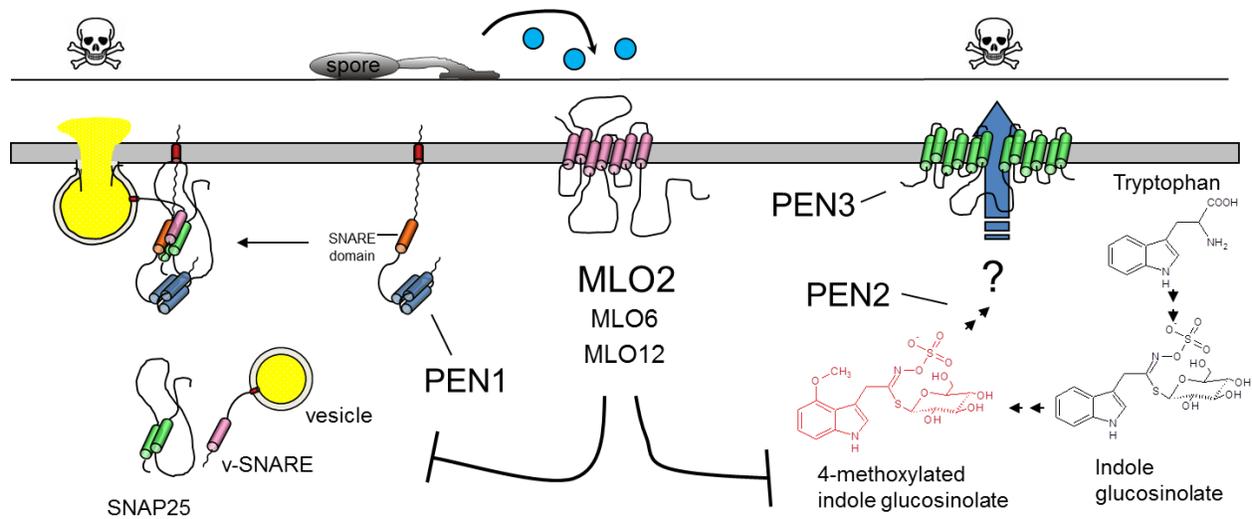


Fig. 3. Model illustrating the proposed defence suppression by adapted powdery mildew fungi via MLO proteins.

Reference

Acevedo-Garcia, J., Kusch, S., and Panstruga, R. 2014. *Magical mystery tour: MLO proteins in plant immunity and beyond. New Phytologist* 204: 273-281.