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Genome-wide association mapping of loci involved in *Potato virus Y* resistance and tolerance in pepper germplasm

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BACKGROUND Plants have evolved two ways to decrease damage induced by parasite infections, resistance and tolerance. Resistance decreases the parasite load within plants whereas tolerance decreases the plant damage for a given parasite load. Resistance itself can be divided into qualitative resistance, usually conferred by a major-effect gene, and quantitative resistance conferred by quantitative trait loci (QTLs). In this study, we tested the following hypotheses:
- In plants, do resistance and tolerance evolve as independent, complementary or alternative defence mechanisms?
- Similarly, do qualitative and quantitative resistance evolve as independent, complementary or alternative mechanisms?

MATERIALS & METHODS We measured the resistance and tolerance levels of 276 accessions representative of the pepper (*Capsicum annuum*) germplasm against *Potato virus Y* (PVY; genus Potyvirus). Two resistance traits were measured in this core-collection: the number of infection foci in plant cotyledons inoculated with a GFP-tagged PVY and within-plant PVY accumulation. Tolerance was measured as the slope of the regression line of PVY-induced damage (plant fresh weight of infected versus mock-inoculated plants) against within-plant PVY accumulation. In addition, genotyping-by-sequencing (GBS) reads were aligned against the reference genome of *C. annuum* cv. CM334 v. 1.55 using the Burrows-Wheeler Aligner tool and the algorithm BWA-MEM. This provided 10,308 single nucleotide polymorphisms (SNPs) covering the whole genome of the accessions.

RESULTS Using these phenotype and genotype data, we performed genome-wide association studies (GWAS) to map PVY resistance and tolerance QTLs in the *C. annuum* genome. We identified four QTLs in the pepper genome that explained a significant proportion of resistance variation and one QTL associated with tolerance variation. These five loci were located on four chromosomes. One resistance locus located on chromosome 4 corresponded to the eIF4E (eukaryotic initiation factor 4E)-encoding gene, which comprises many major-effect alleles in pepper. The confidence intervals of the other QTLs did not include obvious candidate genes for resistance or tolerance. Most of these QTLs coincided with QTLs that had been previously mapped with biparental progenies [1,2]. For each resistance QTL, the favourable allele was associated more frequently than expected at random with favourable alleles at the other resistance QTLs. In contrast, for the tolerance QTL, the favourable allele was less frequently associated with the favourable resistance allele on chromosome 4 than expected at random.

DISCUSSION & CONCLUSION These results show the efficiency of GBS and GWAS in *C. annuum* and indicate highly consistent results between GWAS and QTL mapping using biparental progenies. The fact that resistance alleles at different QTLs were more frequently combined than expected by chance may be explained by an increase in resistance efficiency and/or durability. In contrast, the repulsion observed between resistance and tolerance alleles suggests that, because these defense mechanisms are costly and redundant, plants have to invest either in resistance or tolerance, as suggested by theoretical studies [3].

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