

Extensive genetic variation at the sr22 wheat stem rust resistance gene locus in the grasses revealed through evolutionary genomics and functional analyses

ABSTRACT

In the last 20 years, severe wheat stem rust outbreaks have been recorded in Africa, Europe, and Central Asia. This previously well controlled disease, caused by the fungus *Puccinia graminis* f. sp. *tritici*, has reemerged as a major threat to wheat cultivation. The stem rust (Sr) resistance gene Sr22 encodes a nucleotide-binding and leucine-rich repeat receptor which confers resistance to the highly virulent African stem rust isolate Ug99. Here, we show that the Sr22 gene is conserved among grasses in the Triticeae and Poaceae lineages. Triticeae species contain syntenic loci with single-copy orthologs of Sr22 on chromosome 7, except *Hordeum vulgare*, which has experienced major expansions and rearrangements at the locus. We also describe 14 Sr22 sequence variants obtained from both *Triticum boeoticum* and the domesticated form of this species, *T. monococcum*, which have been postulated to encode both functional and nonfunctional Sr22 alleles. The nucleotide sequence analysis of these alleles identified historical sequence exchange resulting from recombination or gene conversion, including breakpoints within codons, which expanded the coding potential at these positions by introduction of nonsynonymous substitutions. Three Sr22 alleles were transformed into wheat cultivar Fielder and two postulated resistant alleles from Schomburgk (hexaploid wheat introgressed with *T. boeoticum* segment carrying Sr22) and *T. monococcum* accession PI190945, respectively, conferred resistance to *P. graminis* f. sp. *tritici* race TTKSK, thereby unequivocally confirming Sr22 effectiveness against Ug99. The third allele from accession PI573523, previously believed to confer susceptibility, was confirmed as nonfunctional against Australian *P. graminis* f. sp. *tritici* race 98-1,2,3,5,6.

Keyword: Plant biotechnology; Resistance gene; Sr22, stem rust; Ug99; Wheat