

Title

Hybridization speeds up the emergence and evolution of new pathogen species

Eva H. Stukenbrock

Environmental Genomics, Christian-Albrechts University of Kiel, Am Botanischen Garden 9-11, 24118 Kiel, Germany and Max Planck Institute for Evolutionary Biology, August-Thienemann-Str. 2, 24306 Plön, Germany

Abstract (two sentences)

Plant pathogens can evolve new host specificities and overcome host resistances over surprisingly few generations, a process that is greatly accelerated by agricultural practices. A new study provides a striking example in which the rapid emergence of a new pathogen via introgressive hybridization mirrors the evolution of a hybrid cereal crop.

Main text (985 words)

The emergence of a new pathogen

How do new pathogen species emerge and how do new host specificities evolve? Genome based studies have demonstrated that plant pathogens have the potential to diversify and evolve new virulence related traits via extreme levels of genome plasticity and gene or chromosome transfers (1, 2, 3). New population genomic studies demonstrate how hybridization also can provide an important mechanism for emergence of new plant pathogens and novel host specificities over a very short period of time (4).

Menardo and colleagues investigated the evolutionary origin of a new pathogen of the cereal crop triticale (4). Triticale was created in the 1960s by a cross between wheat and rye. Powdery mildew caused by the fungus *Blumeria graminis* emerged as a major disease of this young crop starting in 2001. Other cereal crops including wheat and rye are also infected by *B. graminis*, but by different host specific lineages of *B. graminis* termed *formae speciales*. Population

genomics analyses revealed that the triticale-infecting lineage forms a unique group clearly distinct from the pathogens of wheat and rye; *B. g. tritici* and *B. g. secalis* respectively. However, the *B. g. triticales* genome contains blocks of fixed polymorphisms shared with either *B. g. tritici* or *B. g. secalis*. The only plausible explanation for the mosaic genome structure in *B. g. triticales* is a recent hybridization between *B. g. tritici* and *B. g. secalis* giving rise to a new pathogen of triticale. The new hybrid mildew pathogen inherited the necessary combination of virulence traits from the wheat- and rye-infecting parental species to allow infection of the triticale hybrid host.

Since rye and wheat are co-cultivated throughout Europe, hybridization between mildew pathogens infecting the two crops may have occurred several times. However, the genomic patterns in *B. g. triticales* suggest that the new hybrid was formed from very few interspecific crosses of *B. g. tritici* and *B. g. secalis* followed by two backcrosses with *B. g. tritici*.

The facts that triticale is a young host and mildew was recognized as a disease of this crop only since 2001 imply that the emergence of the *B. g. triticales* hybrid occurred very recently. But the hybrid may have existed for a longer time and only recently infected triticale. By dissecting the frequency of alternating *B. g. tritici* and *B. g. secalis* haplotypes in the hybrid genome, Menardo et al calculated that the mosaic genome of *B. g. triticales* was generated by 7 to 47 recombination events since the initial hybridization. Taking into account the fact that *B. graminis* undergoes one sexual cycle per year, this new triticale pathogen must have originated during the last 50 years.

Key determinants of virulence and host specificity in plant pathogens are so-called effector proteins. Effectors are secreted proteins that interfere with plant defenses and metabolism (5). Genes encoding effector proteins can, among other traits, be predicted by the presence of a signal peptide targeting the protein for secretion (6). The genomes of all analyzed *B. g. triticales* isolates contain a common set of six putative effector genes inherited from *B. g. secalis*. Menardo and colleagues hypothesize that these represent key genetic determinants for the

expanded host range of *B. g. triticales*. However none of the six genes show different expression patterns during infection of wheat and triticales, suggesting that virulence on triticales is determined by additional factors in the hybrid.

Agriculture and hybrid pathogens

The emergence and spread of *B. g. triticales* within the last 10-20 years provides a striking example of how quickly host-specific lineages of plant pathogens – and ultimately new species – can evolve. Hybridization provides a practically instantaneous mechanism for recombining adaptive traits of two species and generating novel phenotypes. Several examples of plant pathogens that originated through interspecific crosses and then invaded new host species have been reported (see review 8). In some cases the hybrids are transient but act as a genetic bridge for the transfer of adaptive traits between parental species (9, 10). In other cases the hybrid evolves as a reproductively isolated lineage (11). For example, the fungal pathogen *Zymoseptoria pseudotritici* emerged from a single sexual cross between two parental individuals (11). *Z. pseudotritici* is a pathogen of wild grasses but a close relative of the prominent wheat pathogen *Zymoseptoria tritici*.

Plant fungal pathogens produce billions of spores and the coincidental encounter of non-conspecific individuals must occur continuously. It is intriguing that both *B. g. triticales* and *Z. pseudotritici* emerged from very few or only one hybridization events. Genomic incompatibilities might hinder the viability of hybrid genotypes. Ecological factors as well as competition with parental species when sharing the same environment can also result in a lower fitness for the new hybrid species. As a result only relatively few unique interspecific combinations at the right time and space can be successful (8). As shown by Menardo and colleagues, agro-ecosystems can be highly conducive for the establishment and spread of such rare but successful hybrid genotypes. The geographical spread of *B. g. triticales* across thousands of kilometers was obviously facilitated by the monoculture of triticales. Not only do agro-ecosystems provide host population on a vast-scale, the genetic and environmental uniformity of these monocultures is highly conducive for the propagation of fit pathogen genotypes (12).

Agricultural trade also brings species together that have not previously co-existed, enabling hybridization. Reproductive barriers between such allopatric species are likely to be more permissive to allow mating between non-conspecific individuals. Thus the human-mediated mixing of allopatric pathogen species increases the chances of hybridization and facilitates the emergence of new host specificities and virulence phenotypes (13). In conclusion, it is important to recognize that hybridization provides an effective mechanism to enable the rapid emergence of new plant diseases. As elegantly demonstrated in the study of *B. g. triticales* (4) population genomics provides a powerful approach to recognize signatures of hybridization in pathogen genomes and to unravel the origin of plant pathogens infecting agricultural crops.

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Figure legend:

Figure 1:

Colony from a single spore of the mildew pathogen *Blumeria graminis tritici* two days after infection of a wheat leaf. The fungal spore and hyphae on the leaf

surface are stained in blue. Below the leaf surface the fungus forms a so-called haustorium (not stained), a feeding structure by which the fungus obtains nutrients from the infected plant cells. Picture by Marion Müller