GENOME WATCH

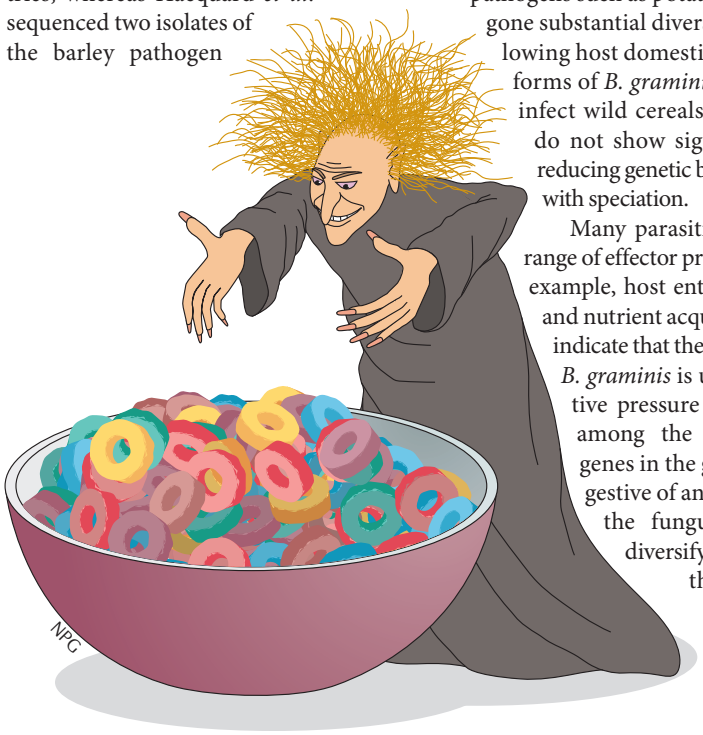
Cereal killers

Thomas D. Otto and Adam J. Reid

This month's Genome Watch traces the evolutionary history of powdery mildew and highlights the 'arms race' of this fungal pathogen with its wheat and barley hosts.

Blumeria graminis is a widespread plant pathogen that causes powdery mildew in grasses, including wheat, barley and other cereals. Two recent studies have examined the evolution of *B. graminis* to reveal high genetic adaptibility and flexibility, which enable this fungus to infect a range of hosts and to overcome host defences.

Powdery mildew fungi are grouped into so-called *formae speciales* (f. sp.) according to their respective host species. Wicker *et al.*[1] sequenced and assembled the genome of *B. graminis* f. sp. *tritici*, which infects wheat, and compared isolates from different countries, whereas Hacquard *et al.*[2] sequenced two isolates of the barley pathogen *B. graminis* f. sp. *hordei* and compared them to an existing reference sequence[3]. In both wheat and barley pathogens, which are separated by ~6.3 million years of evolution, the genomes display a mosaic of evolutionarily young and old haplotypes (regions with relatively few SNPs and regions with many SNPs, respectively). Younger parts of the genome diverged around 10,000 years ago, coinciding with the domestication of the wheat and barley hosts, whereas older parts diverged more than 100,000 years ago during the last ice age, when wild cereals were locally confined.



Both studies suggest that *B. graminis* populations maintain a high level of genetic variation by clonal propagation and infrequent sexual reproduction, thus only rarely breaking up combinations of potentially beneficial alleles that would otherwise be lost by recombination during meiosis. Other crop pathogens such as potato blight have undergone substantial diversifying selection following host domestication. The modern forms of *B. graminis*, however, can still infect wild cereals and their genomes do not show signs of the diversity-reducing genetic bottlenecks associated with speciation.

Many parasitic organisms have a range of effector proteins to mediate, for example, host entry, immune evasion and nutrient acquisition. Both studies indicate that the effector repertoire of *B. graminis* is under positive selective pressure with effector genes among the most polymorphic genes in the genome. This is suggestive of an 'arms race' in which the fungus must constantly diversify its 'weaponry' when the plant becomes resistant to effectors. Hacquard *et al.*[2] used a clever molecular trick to further characterize the role of effectors in host–pathogen interactions. The model plant *Arabidopsis thaliana* is usually resistant to *B. graminis*, but knocking out three immune defence genes makes it susceptible to infection. Resistance can then be reconsituted by supplying the *mildew resistance locus A 1* (*MLA1*) gene from barley. By analysing the transcriptomes of the host and the pathogen, the authors identified two waves of effector gene expression: a first wave during penetration of the plant epidermis and a second during formation of the haustorium (which is a fungal appendage that takes up nutrients from the plant). When the fungus tried to invade the resistant *MLA1*-expressing *A. thaliana*, the second wave of effector genes was downregulated, whereas plant defence genes were upregulated. Interestingly, the effector genes expressed at this stage — early in haustorium formation — are those under the greatest selective pressure, which suggests that this is a key phase of host–pathogen interactions.

These findings provide insight into the ease with which powdery mildew fungi have adapted to infect domesticated cereals and give us clues as to how we might combat them in the future to improve food security.

Thomas D. Otto and Adam J. Reid are at the Sanger Institute, Wellcome Trust Genome Campus, Hinxton, Cambridge CB10 1SA, UK.

e-mail: microbes@sanger.ac.uk

doi:10.1038/nrmicro3144

1. Wicker, T. *et al.* The wheat powdery mildew genome shows the unique evolution of an obligate biotroph. *Nature Genet.* **45**, 1092–1096 (2013).
2. Hacquard, S. *et al.* Mosaic genome structure of the barley powdery mildew pathogen and conservation of transcriptional programs in divergent hosts. *Proc. Natl Acad. Sci. USA* **110**, E2219– E2228 (2013).
3. Spanu, P. D. *et al.* Genome expansion and gene loss in powdery mildew fungi reveal tradeoffs in extreme parasitism. *Science* **330**, 1543–1546 (2010).

Competing interests statement
The authors declare no competing financial interests.