Whole-Genome Analysis of the Journey from Phytopathogen to Biocontrol Agent

Once a pathogen, always a pathogen? Not so—the fungus *Pseudozyma flocculosa* provides an intriguing example of a pathogen that took a different route (reviewed in Bélanger et al., 2012). Initially isolated from a powdery-mildew–infected leaf, *P. flocculosa* acts as a strong antagonist of powdery mildews (Erysiphales) and was thus developed as a biocontrol agent. However, the mechanism by which it affects powdery mildews—whether it acts as a parasite, secretes antibiotics, competes for nutrients, or induces resistance in the host plant—remains unclear. Surprisingly, *P. flocculosa* is classified as a close relative of Ustilaginomycetes fungal pathogens, such as the maize smut *Ustilago maydis*; these biotrophic smut pathogens insert hyphae into the host to feed from cells that remain alive. Also, *U. maydis* and *P. flocculosa* both secrete similar, unusual glycolipids, ustilagic acid and flocculosin, respectively.

To determine where this fungus wandered from the path of pathogenicity, Lefebvre et al. (pages 1946–1959) sequenced and annotated the genome of *P. flocculosa*. Following up on insights derived from the sequencing of the genomes of *U. maydis* (Kämper et al., 2006) and other fungal pathogens, the authors compare the genomes of *P. flocculosa* and its pathogenic relatives. The *P. flocculosa* genome has a higher GC content, and *P. flocculosa* genes have more introns than its pathogenic relatives. In the pathogenic smuts, the mating of haploid fungal cells generates hyphae that then penetrate leaf cells. *P. flocculosa* is not known to mate, and no compatible mate has been found; however, the authors found that its genome retains loci for mating type, meiosis, and sporulation. Thus, it is possible that *P. flocculosa* is, or was once, capable of mating and a sexual cycle. In addition, the *P. flocculosa* genome has a similar set of pathogenicity genes, including cell wall-degrading enzymes and secondary metabolite synthesis enzymes, compared with its pathogenic relatives. These similarities support the idea that *P. flocculosa* evolved from a pathogenic ancestor. However, the authors identified one potentially key difference in the secretome: *P. flocculosa* lacks homologs of nearly all of the *U. maydis* secreted proteins that affect virulence (see figure).

Does this comparison also shed light on the biocontrol functions of *P. flocculosa*? Although production of flocculosin served as an initial explanation for its mechanism of biocontrol, the actual mechanism may involve epiphytic competition, or interference with host-pathogen nutrient transfer. Indeed, although the *P. flocculosa* genome lacks orthologs of most *U. maydis* effectors, it does contain a unique set of secreted proteins that may enable its ability to attack other fungi. For example, one identified protein showed similarity to cytolytic pore-forming proteins and two other proteins resembled loci from *Trichoderma* spp that parasitize other fungi.

The lack of pathogenesis-related effectors can account for the nonpathogenic lifestyle of *P. flocculosa*; however, other intriguing questions remain, including its possible ability to mate, the mechanism by which it attacks other fungi, and the precise role of flocculosin. Examination of the functions of the proteins that are unique to *P. flocculosa* or conserved with its pathogenic relatives will help explain the evolutionary steps that led down the path away from pathogenesis.

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