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Genome Evolution in Plant Pathogens

Peter N. Dodds

Division of Plant Industry, Commonwealth Scientific and Industrial Research Organisation,
Canberra, ACT 2614, Australia

Abstract

Pathogen genes that shut down specific host plant immune responses are highly divergent and have evolved rapidly to accommodate adaptation.

Food security is of global importance and crop diseases caused by plant pathogens are a major constraint to agriculture worldwide. Many of these pathogens have a similar biotrophic life stage during which they contact host cells and secrete effector proteins that alter plant responses to infection (1). In this issue, comparative genomics studies of closely related pathogen species by Raffaele *et al.* on page xxx (2), Baxter *et al.* on page yyy (3), Spanu *et al.* on page zzz (4), and Schirawski *et al.* on page www (5), reveal that such effector proteins evolve rapidly and that their diversity contributes to host range and parasite speciation.

Biotrophic infection strategies have evolved independently in diverse lineages of plant pathogens. These include fungus-like parasites (oomycetes) from the kingdom *Stramenopila*, such as the destructive potato blight pathogen *Phytophthora infestans* (agent of the Irish potato famine), fungi such as powdery mildews (ascomycetes), and rust and smut fungi (basidiomycetes). These pathogens form specialized hyphae (called haustoria) that penetrate the plant cell wall and allow nutrient uptake from host tissue (6). These structures also secrete large repertoires of effector proteins that enter host cells and manipulate defense responses and cellular metabolism. Many oomycete effectors require the short amino acid motif RxLR (Arg, any amino acid, Leu, Arg) for entry into plant cells (7), independently of other pathogen machinery (8,9). Some fungal effectors also enter host plant cells (10,11), although they lack clearly conserved peptide motifs.

Raffaele *et al.* (2) compared the genomes of four very closely related *Phytophthora* species that each infects quite different host plant species (see the figure). The evolution of these pathogens therefore involved relatively recent shifts in host range, followed by specialization to the new hosts. They found most pathogen genes and genome regions to be highly conserved, but genes involved in host-pathogen interaction appear highly diversified, especially the predicted RxLR-containing effectors. Most of these genes are located in gene-sparse, transposon-rich genome regions, suggesting that these features allow rapid evolution of effector loci after host changes. Genes involved in chromatin modification are also located in these regions and show extensive variation, suggesting that epigenetic regulation of gene expression also contributes to adaptation following host shifts.

Despite having a biotrophic life stage, *Phytophthora* species subsequently kill the infected parts of the plant but continue to feed on the dead plant tissue (and can be cultured on simple medium). By contrast, the related oomycete *Hyaloperonospora arabidopsidis*, which is a

pathogen of the model plant *Arabidopsis thaliana*, is exclusively biotrophic and cannot be grown in culture. This pathogen is believed to have evolved from a *Phytophthora*-like hemibiotrophic ancestor. Baxter *et al.* (3) found that its genome contains a unique set of diversified RxLR-containing effectors but has lost many of the hydrolytic enzymes that *Phytophthora* species use to digest host cell walls, as well as many of the genes that induce host cell death. The reduction in these protein classes is inferred as resulting from selection for “stealth,” allowing *H. arabidopsidis* to avoid triggering host defense responses during its extended biotrophic interaction. It is also deficient in metabolic processes that are shared by free-living organisms, such as the lack of nitrate and sulfate assimilation enzymes. Growing exclusively in living plant leaves, *H. arabidopsidis* relies on access to reduced nitrogen and sulfur from host cells.

Likewise, Spanu *et al.* (4) found that the genomes of three species of fungal powdery mildew pathogens (also obligate biotrophs) are deficient in several classes of conserved primary and secondary metabolism genes. These include the nitrate and sulfate assimilation pathways and plant cell wall hydrolytic enzymes, suggesting that the independent evolution to obligate biotrophy that has occurred in the fungal and oomycete lineages involved convergent adaptation to specialize in the exclusively parasitic life-style in plant leaves. The metabolic deficiencies may provide clues for culturing these pathogens in vitro, which so far has proved difficult and hampered research on these organisms. The powdery mildew genomes do not contain RxLR-containing effectors, but encode a unique class of secreted proteins with another conserved amino acid motif, YxC (Tyr, any amino acid, Cys). These genes are highly diverse among the three species, which infect very different host plants, suggesting that most of these effectors are associated with host species-specific adaptation.

In an intriguing twist on these studies, Schirawski *et al.* (5) compared the genome of *Sporisorium reilianum* to that of the related fungal pathogen, *Ustilago maydis* (12), both of which infect maize. Most of the predicted secreted effectors are common to both species, but show much higher divergence than the rest of the genome. Thus, even within a host species, selection imposed by the host immune system or selection that targets different host processes can lead to rapid diversification of pathogen effectors. Most effector-encoding genes are located in small clusters in the genomes of the *U. maydis* and *S. reilianum*, and mutational analysis of these clusters has confirmed their important roles in infection (5,12).

These studies highlight the value of comparative genomics in identifying important virulence genes with host-specific functions. The challenge now is to determine how the effector proteins that these genes encode turn the host cell to their own purposes. What are the specific targets of the effectors in the host and how do they contribute to disease pathogenesis? Understanding the molecular details of the biotrophic life style and plant-microbe coevolution should lead to innovative disease control measures. Some effectors are recognized by components of the plant immune system, a characteristic that is exploited in plant breeding to improve disease resistance of crops. Thus, identifying effectors with important and nonredundant virulence functions that constrain their evolution may allow deployment of more durable resistance sources to safeguard world food production. The recent devastating impact of a new stem rust strain on wheat production in Africa (13) emphasizes the critical importance of developing lasting effective strategies to protect agricultural production from disease threats.

References and Notes

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1. . Agricultural threats

Many pathogens, such *Phytophthora infestans*, target major food crops, such as potato (shown). The genes involved in host-pathogen interactions are highly diversified among related *Phytophthora* species that attack different plants.