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Pathogen effectors shed light on plant diseases

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With the global population expected to increase to 9 billion people over the next 40 years, the question of how to feed the predicted 2.2 billion extra people is now urgent. But how? Suitable farming land is diminishing, climate change is affecting rainfall patterns and soil quality is deteriorating. As we struggle to feed the current population, what are the possibilities for increasing food production by 30%? Advances in agricultural technologies – deployment of fertilisers, pesticides and herbicides, and the increasing adoption of genetically modified crop varieties – have significantly increased yields of some of the world's most important crops. Ongoing challenges include increases in drought tolerance, adaptation to soil nutritional stresses, resistance to high levels of salinity and enhancement of water-use efficiency. But there are other challenges; ~14% of yield in all crops is lost annually to diseases and this figure excludes damage by insect pests (Agrios 2005). According to the latest figures from the International Grains Council (http://www.igc.int/), this correlates to losses of over 270 million tonnes of wheat, maize and rice in 2009.

It is a truism of our field that successful plant pathogens must overcome or manipulate the panoply of plant defences to cause disease. An astonishing series of discoveries over the last 20 years has described the extracellular and intracellular host receptors that detect potential pathogens, and some of the intracellular signalling cascades that formulate the host response. The most important strategy for combating these mechanisms, adopted by all classes of pathogen from viruses to nematodes, is to secrete virulence 'effector' molecules. Depending on the type of pathogen, effectors are able to interdict and suppress host defence mechanisms or actively manipulate them to suit their own infection strategy. Logically, a full description and molecular understanding of these effector strategies will provide us with a full understanding of pathogenicity.

Recent advances in effector biology in nearly all pathogen types have opened our eyes to the complexity of disease development. Through such findings as the translocation of effector proteins in fungi and oomycetes, to discovering the role of effectors in the gene-for-gene nature of necrotrophic diseases, effector biology has now advanced to a point where one can foresee the significant potential of this field in disease management.

This Research Front offers a series of concise reviews by prominent scientists describing recent advances in pathogen effector biology in fungi, oomycetes, bacteria and nematodes. One of the most exciting stories over the last 3 years has been that of the oomycetes, as reviewed by Hardham and Cahill (2010). Here, discovery of a unique peptide motif RxLR defines a class of effectors that are translocated into the host cytoplasm dependent on this conserved motif. The details of this translocation mechanism remain to be characterised but clearly its elucidation is of paramount importance to agriculture. There are vast numbers of these effectors and their roles remain undefined, although evidence suggests that suppression of plant defence will be one important activity.

We also cover the effector proteins of biotrophic and necrotrophic pathogenic fungi, which preserve or kill host tissue, respectively. For biotrophs and hemi-biotrophs, much of the research has focused on *Melampsori linii* (flax rust), *Magnaporthe oryzae* (rice blast) and the smut fungus *Ustilago maydis* (corn smut) (Gan *et al*. 2010). Many effectors identified thus far are traditional 'avirulence' gene products, whose recognition by the host results in the hypersensitive cell death response. These include AvrL567 and AvrM from *M. linii* and Avr-Pita from *M. oryzae*, all of which interact directly with corresponding host receptors. As for oomycetes, the translocation of effectors from biotrophic and hemi-biotrophic fungi into the host cytoplasm has been demonstrated, although the mechanism remains unresolved. Unlike the oomycete effectors, conserved domains analogous to the RxLR motif have yet to be identified. Also covered in this series are extracellular effectors that act outside the host cell (Catanzariti and Jones, 2010). These include the well-studied Avr proteins of *Cladosporium fulvum* and the intriguing secreted in xylem (Six) proteins of *Fusarium oxysporum* f. sp. *lycopersici*.

Necrotrophic fungi have emerged as dominant pathogens recently due to the emergence of no-till farming practises – a classic example of the contrasting pressures on modern agriculture. The wheat pathogens *Pyrenophora tritici-repentis*, *Stagonospora nodorum* and *Mycosphaerella graminicola* cause serious yield losses globally (Tan *et al*. 2010). Until recently, necrotrophs were considered to be simplistic pathogens that rely upon a battery of lytic enzymes to degrade host tissue and scavenge the remains. Research has now shown that this isn't so and that these fungi do interact with their hosts in a gene-for-gene manner as do biotrophs, albeit inversely. This work has now advanced to the point where plant breeders can use purified necrotrophic effector proteins to identify the presence of corresponding susceptibility loci by the presence of a characteristic cell death response, a technique dubbed effector-based breeding.

Finally, we consider the effectors of bacteria and nematodes. Considerable research has been undertaken on bacterial effectors, and we gain much of our understanding of pathogenicity from detailed descriptions of the molecular actions of bacterial

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effectors (Gimenez-Ibanez *et al*. 2010). As with many oomycete and fungal effectors, the bacterial effectors act intracellularly and, although it is now well understood how they enter host cells, there still remains much to learn about bacterial effector strategies and mechanisms. In contrast to the mature field of bacterial effectors, nematode effectors have only recently been identified (Hassan *et al*. 2010). Two roles are emergent – effectors seem to facilitate host cell reprogramming to establish the specialised feeding structures that are characteristic of the sedentary nematodes and probably also target host signalling pathways. The contribution of nematodes to agricultural yield losses is highly significant, so understanding their effector biology will surely enhance disease management strategies.

The pathogen effector field has revolutionised our understanding of plant diseases. These fast-evolving proteins show how evolution can provide rapid answers to some of the most challenging questions in biology – the trench warfare (or antagonistic co-evolution) at the heart of the plant–pathogen interface. These concise reviews provide a current snapshot of the field and provide an excellent resource for students and experienced researchers.

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