CHAPTER 3

Comparative Genetics of Avirulence and Fungicide Resistance in the Powdery Mildew Fungi

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3.1. Introduction

The powdery mildew fungi cause important diseases of many crops and wild plants, but research on their genetics in the last 50 years has concentrated on just one species, *Blumeria graminis* (syn. *Erysiphe graminis*), the powdery mildew pathogen of cereals and grasses.1 In the earliest work on the genetics of powdery mildews, however, a much wider range of species were studied (Harper 1905), while the most detailed studies of the cytology of these fungi were done on *Phyllactinia guttata* (syn. *P. corylea*) (Colson 1938). Research on *B. graminis* developed strongly in the 1950s, when Moseman and colleagues began to investigate gene-for-gene interactions between isolates of *B. graminis* and varieties of barley and wheat (Moseman 1966; Jørgensen 1988). Barley powdery mildew is now one of the best-understood fungal diseases of plants in terms of the genetics of the host-pathogen interaction. Research on the molecular genetics of *B. graminis* f.sp. *hordei*, the barley mildew fungus, has developed rapidly in recent years, with procedures for transformation (Chaure et al. 2000), construction of DNA libraries (Borbye and Giese 1994), and development of genetic maps based on DNA markers (Christiansen and Giese 1990; Brown and Simpson 1994).

1The generic names used in this chapter follow the recommendations of Braun et al. (2001). The older, and generally better known, synonyms are given at the first mention of a species.

3.2. Avirulence

3.2.1. Gene-for-gene interactions

3.2.2. The gene-for-gene relationship in cereal mildew

3.2.3. Multiple avirulence genes

3.2.4. Modifiers of avirulence

3.2.5. Mechanisms of resistance

3.2.6. Exceptions to the gene-for-gene model

3.2.7. Gene-for-gene interactions in other powdery mildews

3.2.8. Why is gene-for-gene resistance not found more often?

3.3. Fungicide resistance

3.3.1. Genetics of resistance in barley mildew

3.3.2. Fungicide resistance in wheat mildew

3.3.3. Fungicide resistance in other powdery mildews

3.3.4. Mutation in the eburicol 14α-demethylase gene

3.4. Is *Blumeria graminis* f.sp. *hordei* a model powdery mildew?

The genetics of *B. graminis* have presented serious challenges to researchers, because, as the fungus is an obligate biotroph, the range of characters that can be studied is limited. In such common laboratory fungi as *Neurospora crassa* and *Aspergillus nidulans*, phenotypic variation in colour, morphology, and auxotrophic requirements has been used extensively in genetic analysis, but this is not possible in *B. graminis*. The two sets of phenotypic characters that have been studied in the most detail are those that are most important for the adaptation of the fungus to its host, namely race-specific avirulences and responses to fungicides.

Barley mildew is sometimes regarded as a model for research on other powdery mildews and even for biotrophic fungal diseases of plants in general. Such claims that one organism or another is a model system for a larger group should be subject to as rigorous a test as any other hypothesis in biology. With this in mind, this chapter considers the relevance of research on the genetics of *B. graminis*, especially f.sp. *hordei*, to other powdery mildew fungi. In the best-studied species of dicot-infecting powdery mildews, variation is known in avirulences and responses to fungicides, while genetic research on some mildew fungi, notably *Erysiphe necator* (syn. *Uncinula necator*, grapevine powdery mildew) and *Podosphaera xanthii* (syn. *Sphaerotheca fulginea* auct. p.p.), one of the mildew pathogens of cucurbits, is progressing. It is therefore timely to consider, on the one hand, the extent to which knowledge about the genetics of avirulence and fungicide resistance may be extrapolated from one powdery mildew fungus to another and, on the other hand, what limitations there might be in the concept of *B. graminis* f.sp. *hordei* as a ‘model powdery mildew.’