

# Genetic and forma specialis diversity in *Blumeria graminis* of cereals and its implications for host-pathogen co-evolution

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## SUMMARY

The grass powdery mildew fungus, *Blumeria graminis* is classified into eight formae speciales (ff.spp.) based on strict host specialization. However, evidence suggests that host ranges extend to more than one genus and are particularly diverse among samples from the Middle East, the proposed centre of origin and diversification of crop plants. This study investigated whether geographical origin, host species or both determine the genetic variation in *B. graminis* that is found in cereals, sampled from Europe, Asia and North America, and whether there is any evidence for co-evolution between pathogen and host. Phylogenetic analysis of nucleotide sequence variation within the ribosomal DNA Internal Transcribed Spacer (ITS) regions and the  $\beta$ -tubulin (*tub2*) gene gives rise to two dendrograms with different topologies. In both trees, isolates of *B. graminis* from cultivated cereals are grouped according to their principal host genus. This grouping was supported by amplified fragment length polymorphism (AFLP) analysis and cross-infectivity tests. However, there was no evidence of co-evolution. There was far greater divergence between ff.spp. in *tub2* sequences than ITS regions and a faster rate of mutation of *tub2*, especially in the third base position of exons. It is proposed that variation in the rDNA-ITS regions is constrained either by their functional role in the processing of rDNA precursor molecules or by concerted evolution, hence limiting their use in phylogenetic studies. AFLP data suggests an overall lack of correlation between geographical and genetic distances. This may be related to the long distance dispersal exhibited by *B. graminis*.

## INTRODUCTION

Biological specialization, the ability of a fungal species or race to infect and reproduce only on a particular host or group of hosts (i.e. host range specialization, Leppik, 1965), is characteristic of biotrophic fungi such as powdery mildews, rusts and smuts (Parlevliet, 1986). Biological specialization has been used as a

basis for taxonomic classification of hosts and parasites (Johnson, 1968; Meeuse, 1973; Mitter and Brooks, 1983; Raper, 1968; Savile, 1954) and may form part of the process of co-evolution (Futyuma, 1996) between a pathogen and its host.

The obligate, biotrophic fungus *Blumeria graminis* (DC) Speer (Syn. *Erysiphe graminis* DC) is the causal agent of powdery mildew in cereals. Strict host specialization was described for *B. graminis* by Marchal (1902), with infection limited to a single host genus. This formed the basis of a classification system delimiting seven formae speciales (ff.spp.), which was extended to eight by Oku *et al.* (1985). These include *B. graminis* f.sp. *hordei* on species of *Hordeum*, f.sp. *tritici* on *Triticum*, f.sp. *secalis* on *Secale*, f.sp. *avenae* on *Avena*, and four ff.spp. on wild grasses. Subsequent studies have shown that the host ranges extend to plants from more than one genus and even to other tribes (Eshed and Wahl, 1970; Hardison, 1944; Hirata, 1966; Sheng *et al.*, 1995).

Eshed and Wahl (1970) found that the host range of *B. graminis* varied according to the geographical area from which it was sampled. Isolates from cereals in Israel had a wider host range than those from elsewhere in the world, reflecting the greater genetic diversity of host plants in the Middle East, the proposed centre of origin and diversity of the wild ancestors and relatives of cultivated cereals. This association suggests the possibility of correlated evolution between *B. graminis* and its cereal hosts, and indicates that the formae speciales concept needs to be investigated in terms of geographical origin.

When the systematic relationship of a pathogen reflects that of its host, their evolutionary histories may also be linked. This is summarized by Fahrenholz's rule, 'parasite phylogeny mirrors host phylogeny' (Eichler, 1948), which assumes that a pathogen species may be associated with a host species because it or its ancestor was associated with the host's ancestor, implying that speciation in the host and parasite is approximately simultaneous. However, the ability of a pathogen to infect different host genera may not reflect host phylogeny. The geographical origin of the host and expansion of its range may affect the host range of a pathogen, such that hosts coexisting in close proximity may be exposed to attack by the same pathogen irrespective of their phylogeny (Eshed and Dinoor, 1980; Eshed and Wahl, 1970).

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