

Clonality and long-distance migration of *Puccinia striiformis* f.sp. *tritici* in north-west Europe

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The biotrophic fungus *Puccinia striiformis* f.sp. *tritici*, a basidiomycete that causes yellow rust on wheat, is spread by wind-dispersed spores. Analysis of amplified fragment length polymorphism (AFLP) variation showed that the fungus frequently migrates between the UK, Germany, France and Denmark. There is no biological evidence for sexual or parasexual reproduction under natural conditions, and this was supported by the lack of recombination, as revealed by AFLP, over the time and area represented by the samples in this study. A phylogeographic analysis revealed that there was effectively a single, clonal population in the four countries, up to 1700 km apart, consistent with a ‘continent-island’ model in which Denmark is the recipient of migrants from other countries. In five cases, specific pathogen clones were dispersed between the UK and Denmark, and on at least two recent occasions clones were also spread from the UK to Germany and France, causing outbreaks of yellow rust on wheat cultivars that were previously resistant to the disease in these countries. The agronomic consequences of migration were enhanced because of the limited genetic diversity for yellow rust resistance in wheat cultivars in the area. These results demonstrate that long-distance migration of pathogen clones, coupled with low diversity in the host species, may cause previously useful resistance genes to become ineffective for disease control on a continental scale.

Keywords: AFLP markers, evolution of virulence, molecular diversity, monoculture, spore dispersal, wheat yellow rust

Introduction

Spores of fungal plant pathogens may be spread by wind over long distances, either in a single step or in several successive steps, thereby enhancing disease epidemics across large areas, e.g. wheat yellow rust (Zadoks, 1961) and coffee leaf rust (Bowden *et al.*, 1971), wheat stem rust (Roelfs, 1986), barley stripe rust (Dubin & Stubbs, 1986) and potato late blight (Goodwin *et al.*, 1992). The emergence of new molecular techniques for fingerprinting individual organisms, such as fungal isolates, has greatly increased the possibility of detecting such migration in populations of plant pathogens (Brown, 1996; Milgroom, 1997).

Wheat yellow rust is caused by the basidiomycete fungus *Puccinia striiformis* f.sp. *tritici*. There is no evidence that the fungus, which is biotrophic, completes a sexual reproductive cycle, as no alternate host has been identified, unlike many other cereal rusts (Stubbs, 1985). It is

spread by dikaryotic urediniospores, and there are many indications that the spores are dispersed over wide areas. In Europe, live spores of the fungi that cause powdery mildew and brown rust of barley and wheat were wind-transported for at least 600 km across the North Sea, between the UK and Denmark (Hermansen *et al.*, 1978). Transport of spores that cause yellow rust of wheat was not demonstrated directly, but the epidemics of wheat yellow rust on wheat in Denmark in 1971 and 1972 may have been initiated by spores blown across the North Sea (Hermansen & Stapel, 1972).

The diversity of races or pathotypes, common concepts in studies involving gene-for-gene interactions between host and pathogen, is often low in *P. striiformis* f.sp. *tritici* populations, although it may vary considerably between region, year and host cultivar (Stubbs, 1985; Hovmøller, 2001). The mechanisms by which new variation is created in *P. striiformis* are not fully understood, but mutation from avirulence to virulence is generally considered to occur fairly frequently (Wellings & McIntosh, 1990). Formation of new pathotypes by reassortment of whole nuclei has been observed in experiments where host plants were inoculated with two different pathotypes (Little & Manners, 1969a; Wright & Lennard, 1980). In another

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