Evolution of barley powdery mildew pathotype frequencies in field populations between sowing and oversummering

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Evolution of Barley Powdery Mildew Pathotype Frequencies in Field Populations Between Sowing and Oversummering

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Role of primary inoculum in determining pathotype frequencies in barley powdery mildew populations was studied in a field experiment. Three *B. graminis* f. sp. *hordei* isolates belonging to pathotypes that were rare in the local aerial inoculum were used to inoculate field plots. Treatments on the field plots included two successive inoculations, performed at a two-generation delay. Eventhough barley powdery mildew was known for its frequent long-distance dispersal and its large amount of natural airborne inoculum, it was possible to follow the frequencies of the inoculated pathotypes over the barley growing season. Frequencies of pathotypes in the resulting population depended mainly on the time of arrival of inoculum on the plot: the earliest inoculated pathotypes were always the most frequent, and we called this an "early-arrival" effect. A genotype effect was also observed among the three isolates used. A two-generation delay was sufficient to create a shift in pathotype frequencies, and this shift was not compensated during the whole epidemics on the crop.

As opposed to the low amount of evolution in pathotype frequencies within populations established on the crop, a high variability among replicated situations was observed during the transition from crop to volunteers. The frequency of a pathotype on volunteers was not correlated to its frequency in airborne population, to frequency on the plot before summer, or to expected frequency assuming random association of virulences.

Keywords: *Blumeria graminis,* powdery mildew, barley.

Understanding pathogen population structure and evolution is needed to design management practices able to limit apparition and spread of virulent and fungicide-insensitive clones of the pathogen. To-date, populations of *Blumeria (Erysiphe) graminis* f. sp. *hordei,* became rapidly adapted to all but the *mlo* resistance genes used in barley varieties, and to chemical groups of fungicides. Epidemiological characteristics, including recombination and efficient dispersal, contributed to this high potential of adaptation. Life cycle of the fungus allows 15 to 20 asexual generations over the course of a barley growing season and one optional sexual generation in summer could favour the selection of new pathotypes. Airborne migration of spores, described over large distances could favour the spread of new pathotypes.

Between two successive growing seasons, large changes can occur rapidly. During the barley growing season, selection by resistance genes used in varieties is strong. Few changes in population structure were observed over one growing season. But in natural populations, once populations were established on a field, the high pathotype diversity prevented recognition of the origin of inoculum. In spring, airborne inoculum produced on winter varieties was postulated to be source of infections on newly-sown spring varieties. However, contradictory opinions about the period of time during which population structure

0238–1249/2000/$ 5.00 © 2000, Akadémiai Kiadó, Budapest

on a newly-sown field is influenced by airborne spore population were published. Based on spore contents of the air, influence of airborne inoculum was postulated to be important almost all year round (Limpert et al., 1999). Based on proportions of virulent and avirulent spores sampled above a field, relative importance of immigration rapidly decreased when epidemics started (O'Hara and Brown, 1996).

We designed a field experiment using two successive artificial inoculations with three *B. graminis* f. sp. *hordei* isolates. First part of the experiment aimed to study the influence of arrival of inoculum during the establishment of the epidemics on resulting population structure, and evolution during the epidemics on the crop. Advantage of the early-arrived isolates and influence of isolates used on pathotype frequencies in resulting populations were quantified at the start of the epidemics. A second sampling was performed at the end of the epidemics to test for the persistence of the two effects during the whole barley growing season. Second part of the experiment focussed on the transition of powdery mildew populations from the crop to the volunteers of the same plot. An additional sampling was performed in summer from airborne population and populations established on volunteers.

Materials and Methods

Experiments started shortly after emergence of the barley plants. In each of the four replicates, two successive inoculations with three single-spore isolates were performed at a two-generation delay to get various inoculation-date/isolate combinations in the nine field plots. Number of generations was estimated from the duration of the latent period as a function of mean temperature. The three isolates were selected for the experiment because they belonged to pathotypes that were rare in the local mildew population at the start of the experiment. Frequencies of pathotypes in the powdery mildew populations from each plot were assessed twice on the crop, four and nine generations after first inoculation, and one time on volunteers.

Isolates were tested on a eight-resistance genes differential set that allowed to recognize the three inoculated pathotypes from the local natural powdery mildew population. On the crop, the effects of isolate, of inoculation date and stability of both over time were tested by analysis of variance.

The influence (i) of airborne population, (ii) of the populations of conidia present on the crop, on pathotype frequencies in populations of conidia present on volunteers were investigated by correlation analysis between frequencies of the three inoculated isolates in air, crop and volunteers samples from all plots in two of the replicates (18 plots). Correlation was also assessed between observed frequencies on volunteers and expected frequencies assuming random association of alleles.

Results and Discussion

In experiments with natural populations, it is not possible to know retrospectively when each clone arrived on the plot. This information was made available by using two successive inoculations. Considering one isolate, frequency of the resulting pathotype in the established population was significantly different depending on the time of arrival on the plot, eventhough the same inoculum load was transplanted in each plot. Considering one field plot, first-arrived clones were the most frequent in resulting populations. There were differences between the three isolates used, but apart from two exceptions early arrival effect always prevailed over genotype effect in resulting frequencies in the established population. Early-arrival effect was observed in all locations independently of their sowing time. These results confirmed the epidemiological importance of early-arrived inoculum. We were able to precise that a two-generation delay was sufficient to create a shift in frequencies of pathotypes. This would imply that the time period during which the field population is sensitive to the immigration of airborne inoculum is restricted in time. Further experiments should be carried out to study the interaction between disease level and relative importance of immigration.

Observed increase in the magnitude of the genotype effect during the epidemics on the crop was smaller than initial differences between isolates. Transplantation time of the isolates on the plot influenced pathotype frequencies throughout the whole epidemics. Magnitude of the early-arrival effect was not reduced after nine generations, and first-arrived isolates were still more frequent than those transplanted two generations later. These results contributed to understand how accurate predictions on evolutions in populations were obtained with models regarding dispersal of the airborne spore populations on cultivars as a single event during growing season (e.g. Østergård and Hovmøller, 1991; Hovmøller et al., 1993).

The study included 18 field plots, with a range of frequencies of the three pathotypes in populations established on the crop before summer. Comparing many populations during their transfer from crop to volunteers (repetitions) allowed to reveal the high variability detected in frequencies of the pathotypes on volunteers, among plots placed in similar environmental conditions. Previous field studies on natural populations allowed to detect changes in pathotype diversity (e.g. Welz and Kranz, 1987) but not to recognize the differences in evolution of pathotype frequencies occurring between transitions from crop to volunteers on many repetitions. Variability in pathotype frequencies on volunteers was neither correlated to frequencies in aerial population, nor to frequencies in conidial populations on the crop before summer or to expected frequencies assuming random association of virulence alleles. This indicated that during summer survival chance events might have a large influence on pathotype frequencies. These results were in agreement with observations of the dynamics of pathotypes in field populations sampled repeatedly during the growing season (Bousset, 2000) and contribute to understand how large changes in pathotype frequencies could occur from one growing season to the next.

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