Eleventh EuroBlight workshop
Hamar (Norway), 2008

Invasion of a Virulent *Phytophthora infestans* Genotype at the Landscape Level; Does Spatial Heterogeneity Matter?

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SUMMARY

Proper landscape-scale deployment of disease resistant genotypes of agricultural crop species could make those crops less vulnerable to invasion by resistance breaking genotypes. Here we develop a multi-scale, spatiotemporal model of the potato late blight pathosystem to investigate spatial strategies for the deployment of host resistance. This model comprises a landscape generator, a potato late blight model, and a suite of aerobiological models, including an atmospheric dispersion model. Within individual growing regions, increasing the number of host genotypes caused the greatest reduction in epidemic extent, followed by reduction of the proportion of potato in the landscape, lowering the clustering of host fields, and reducing the size of host fields. Deployment of host resistance in genotype mixtures had a large effect on disease invasion.

The use of space as an isolation barrier was effective in scenarios involving two distinct potato growing regions. It was possible to completely eliminate the risk of epidemic spread from one region to another using inter-regional separation distances ranging from 8 to 32 km. The overall efficacy of this strategy was highly dependent, however, on the degree of spatial mixing of potato genotypes within each region. Deployment of host resistance in genotype mixtures in both regions served to reduce the overall level of incidence in the landscape and the inter-regional separation distance required to eliminate relevant levels of between-region spread of disease.

KEYWORDS

Phytophthora infestans, invasion, Gaussian plume model, landscape design

INTRODUCTION

Crop heterogeneity can profoundly affect epidemics caused by the transmission of infectious agents (e.g., Zhu *et al.*, 2000). Landscape design and strategic deployment of host resistance therefore emerge as a means to spatially separate aggressive resistance-breaking pathogen genotypes from other susceptible local host populations. In this paper we raise an important question regarding the spatial epidemiology of *Phytophthora infestans* – does spatial heterogeneity in host populations matter, and if so, what scale is relevant?

PPO-Special Report no. 13 (2009), 97 - 102

We describe a simulation framework to investigate which spatial strategies reduce the development of epidemics when a breakthrough of resistance occurs in a proportion of the host population, i.e., when a new, aggressive strain of the pathogen evolves. The framework comprises a recently validated potato late blight model (Skelsey *et al.*, in press) and a suite of aerobiological models, including a long range atmospheric spore dispersion model. Invasion opportunities of virulent pathogen genotypes are assessed under a variety of historical weather conditions and theoretical landscape configurations. The effects of landscape characteristics are studied using scenarios that vary a potato growing region (1 region scenarios) using a limited set of design parameters, and two spatial scales of mixing of host genotypes: genotype mixing *within* a field or *between* fields. Invasion opportunities of virulent pathogen genotypes are also assessed at larger spatial scales using scenarios that vary the separation distance between two distinct potato growing regions (2 region scenarios). In the 2 region scenarios, an additional spatial scale of genotype mixing is simulated; *between-region* mixing, whereby each region is homogeneous for a particular potato genotype.

MATERIALS AND METHODS

Simulation framework

Host and pathogen life cycles, host-pathogen-environment interactions, and fungicide applications (protectants and eradicants) are simulated on gridded (raster) landscapes composed of potato and non-potato areas. The number, size, aggregation and classification of potato fields can be varied. In the 1 region scenarios, each potato growing region measures 6.4 x 6.4 km. In the 2 region scenarios, each potato growing region measures 2 x 2 km, with a variable amount of non-potato area between them.

An adaptation of the spatiotemporal/integrodifference equation model of the potato late blight pathosystem originally developed by Skelsey *et al.*,(2005) is used to provide field-scale dynamics. In this study, two potato phenotypes are represented: susceptible and (partially) resistant. The susceptible phenotype represents the genotype with the broken resistance, while the other phenotype represents all other (partially) resistant genotypes. Partially resistant varieties can still become infected, although the rate of infection is far reduced in comparison to the 'broken' or susceptible genotype. Host-pathogen interactions are characterized in the model using quantitative components of resistance (lesion growth rate, sporulation intensity, and infection efficiency) measured in the laboratory on potato leaflets of two cultivars, providing parameter values for the susceptible (broken) and the (partially) resistant interaction (Skelsey *et al.*, in press). The field-scale potato late blight model was recently validated for these and other cultivar-isolate interactions using data from field trials in the Netherlands (Skelsey *et al.*, in press).

Individual fields in the landscape are linked through models describing: spore release from sporangiophores; spore escape from the canopy (de Jong *et al.*, 2002); spore dispersion and deposition (partial-reflection Gaussian plume model - Overcamp, 1976); and spore survival during transportation, according to the dose of global radiation received (Mizubuti *et al.*, 2000).

Within this modeling framework, the composition, configuration and connectivity of host populations are manipulated in order to reveal their influence on epidemic progress. The results of these manipulations are used to develop spatial strategies for the deployment of resistance genes.

Spatial scenario analyses – 1 region scenarios

Four basic scenario analyses are defined. These analyses address the influence of: (1) the proportion of potato in the landscape; (2) the number of different resistant potato genotypes; (3) the size of fields; and (4) the degree of spatial clustering of potato fields on the rate and extent of invasion of a new, resistance breaking *P. infestans* genotype. In these scenarios, potato genotypes can be deployed at two spatial scales of mixing. Under the first scheme, designated 'between-field mixing,' each

Table 1. Spatial parameter values defining the five sets of spatial scenarios

1 region scenarios					
Scenario analysis	Region size (km)	Proportion of potato in the region (-)	Susceptible proportion of the population (-)	Field size (ha)	Spatial pattern of fields (-)
1	6.4 x 6.4	1/64, 1/16, 1/4, 1	1/4	1	Random
2	6.4 x 6.4	1/4	1/64, 1/16, 1/4, 1	1	Random
3	6.4 x 6.4	1/4	1/4	1, 4, 16, 64	Random
4	6.4 x 6.4	1/4	1/4	1	Clustered (scale = 0 to 1)
2 region scenarios					
Scenario analysis	Region size (km)	Proportion of potato in each region (-)	Susceptible proportion of the population (-)	Field size (ha)	Separation distance between regions (km)
5	2 x 2	1	1/2	4	0, 1, 2, 4, 8, 16, 32

individual field in the landscape contains a single host genotype; either resistant or susceptible. Under the second scheme, designated 'within-field mixing,' each field contains a mixture of resistant and susceptible varieties, i.e., a genotype mixture.

2 region scenarios
The use of space as a barrier to pathogen invasion from one potato growing region to another is investigated in '2-region scenarios.' This scenario analysis addresses: (5) the influence of the separation distance between two growing regions on epidemic extent. One region is the 'donor' (infected), and the other the 'receptor' (disease-free). In addition to simulating both the between-field and within-field mixing schemes, a third level of genotype mixing is included: 'between-region mixing,' whereby the donor region is entirely composed of the susceptible potato phenotype, and the receptor region is entirely composed of the resistant potato phenotype. The spatial parameter values defining all 5 sets of spatial scenarios are given in Table 1. The parameter setting defining landscape maps, as in Table 1, in combination with the spatial scale of mixing genotypes, defines a scenario.

RESULTS AND DISCUSSION

The results of this study indicate that spatial heterogeneity in host populations does matter for *P. infestans*, and that landscapes can be designed that suppress invasions of virulent pathogen genotypes. The more effective of the strategies tested for individual growing regions were those that increased the number of potato genotypes, and/or increased the degree of spatial mixing of genotypes, i.e. within-field genotype mixing (Fig. 1). Landscape designs that focused on spatial isolation of aggressive pathogen strains through manipulation of field size and clustering of potato fields were found to have limited effect. There was little evidence of thresholds in the response of epidemics to manipulation of spatial landscape variables, i.e., in the 1 region scenarios, no situations were identified in which spatial design had quantum effects on the prevalence of *P. infestans*.

The use of space as an isolation barrier was effective in the 2 region scenarios, but the efficacy of this strategy was again dependent on the degree of spatial mixing of potato genotypes (Fig. 2).

The results of the 2 region scenarios act to confirm the scant information in the literature on the large capacity of *P. infestans* for long distance dispersal (e.g., Zwankhuizen *et al.*, 1998; Mizubuti *et al.*, 2000; Sunseri *et al.*, 2002). Nevertheless, it was possible to completely eliminate the risk of epidemic spread from one region to another. Geographic separation of growing regions according to potato phenotype (between-region mixing) was particularly successful in this respect, with a

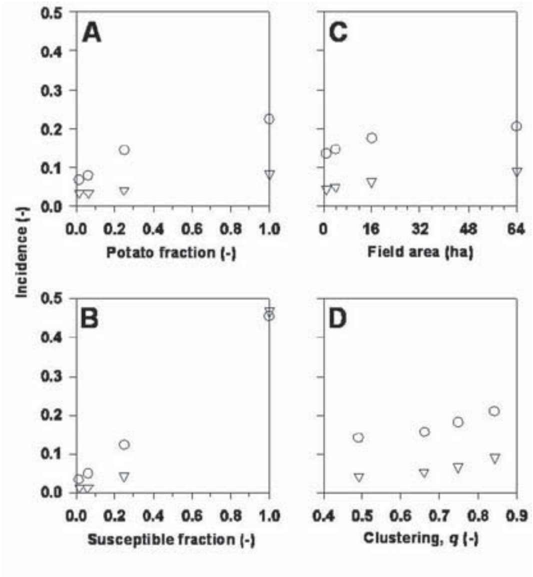

Figure 1. Influence of spatial host population characteristics on the spatial extent of simulated potato late blight epidemics within individual growing regions. Panels A to D correspond to spatial scenario analyses 1 to 4 (Table 1). Incidence is defined as the number of potato hectares infected (disease severity ≥ 1%) relative to the number of potato hectares in the landscape. Circular data markers show predictions for the between-field genotype mixing scheme, and triangular data markers show predictions for the within-field genotype mixing scheme.

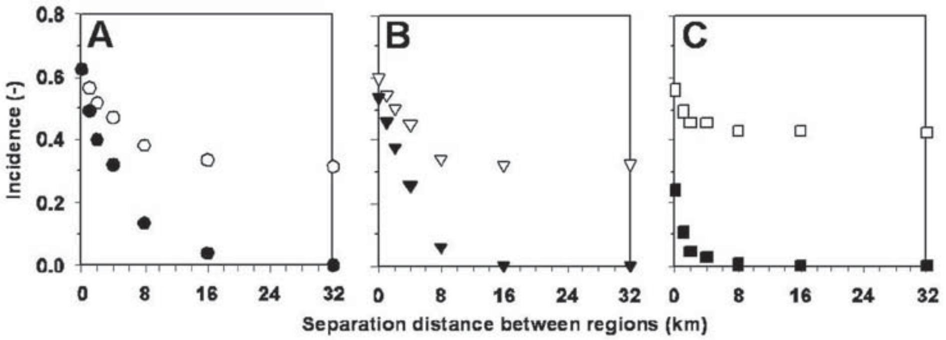

Figure 2. Influence of inter-regional separation distance and spatial scale of mixing of potato genotypes on the spread of potato late blight disease from a 'donor' (inoculated) to a 'receptor' (disease-free) potato growing region (Table 1; scenario analysis 5): (A) between-field genotype mixing; (B) within-field genotype mixing; and (C) between-region genotype mixing. Incidence is calculated in two ways: open data markers show the number of potato hectares infected (disease severity ≥ 1%) relative to the number of potato hectares in the landscape, and solid data markers show the number of potato hectares infected in the receptor region relative to the number of potato hectares in the receptor region.

complete elimination of between-region spread at a separation distance of 8 km. As landscape planners, however, we must concern ourselves with the total amount of disease in the landscape (both donor and receptor regions). Landscape incidence levels were markedly reduced when the degree of spatial mixing of potato genotypes within regions was increased.

CONCLUSIONS

In combining this knowledge, we arrive at a unified spatial strategy for deployment of host resistance, with a view to suppressing invasions of a virulent strain of *P. infestans*: landscape-wide, homogenous (non-aggregated) deployment of diverse genotype mixtures in small fields. Simulation results suggest that this strategy would be effective in reducing spatial increase in disease within and between growing regions, and thus in minimizing the consequences of a breakthrough in resistance. Secondary effects could include an increase in the performance and durability of resistance, and a reduction in the need for plant protection products.

ACKNOWLEDGEMENTS

Funding for this study was provided by the Dutch Ministry of Agriculture, Nature Management and Fisheries through the DuRPh project - theme: "Resistance management," project no. 3340043100, and through the Umbrella Plan Phytophthora (DWK 427). Thanks to Joost de Groot for his help with the computer cluster.

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