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The Canon of Potato Science:

32. Variety Mixtures and Diversification Strategies

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What are they?

Diversification of resistance is an ecological approach to restrict plant diseases through functional diversity. Functional diversity is diversity that limits pathogen and pest expansion and that is designed to make use of knowledge about host-pest/pathogen interactions to direct pathogen evolution. Diversification strategies for potato encompass mixed cropping in the form of randomly mixed varieties, alternating rows or strips of varieties, or strip intercropping of potato with other crop species.

The three most important factors contributing to disease reduction in diversified stands are: a) dilution of inoculum, where there is an increased distance between plants of the same susceptibility for a particular pathogen genotype; b) barrier effects, with resistant plants acting as barriers to pathogen spread; and c) induction of host defence mechanisms by avirulent spores preventing or delaying infection by adjacent virulent spores. Interactions among pathogen races and plant varieties or species may enhance or reduce these effects, depending on the hosts and pathogens involved.

Intimate mixing of varieties is being used successfully in several cropping systems such as small grained cereals but also for coffee and other crops. A number of key characteristics of host-pathogen systems have been identified that contribute

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to the success of diversification strategies: a) a small genotype unit area by which is meant the area of a patch in the crop in which plant tissue has identical genetic composition for resistance; b) a shallow dispersal gradient of pathogen spores; c) small lesion size; d) short pathogen generation time; and e) strong host specialisation. While not all these properties have to be present at the same time, the potato-late blight system lacks several: potato plants are large and have broad leaves, *Phytophthora infestans* causes large spreading lesions, most functional potato resistance to *P. infestans* is considered race non-specific, and resistance is difficult to induce in potato. Despite these limitations, recent research showed that patterns of diversification (including the use of non-hosts and making use of local wind patterns) and plot size effects on initial infections and on disease progress rates may have significant effects on late blight epidemics and thus on yields.

Why are they Important in Potato Science?

P. infestans is notorious for its ability to quickly adapt to newly released resistances and also for the development of resistance to fungicides. Thus, there is a need to reduce epidemic pressure to reduce fungicide applications and thus the speed of adaptation as much as possible. This will, on the one hand, slow down the loss of resistances and fungicides. On the other hand, it will help to produce potatoes under low or minimum input conditions where farmers either have no access to, or finances to buy, fungicides or, for example in organic production systems, where only less effective or no fungicides are available.

Spatio-temporal effects of diversification strategies are of particular relevance here to develop new concepts in theory and practice.

Why are they Important for the Potato Industry?

Variety mixtures are considered primarily to be a way of delaying epidemic development through the dynamic use of genetic resources. The agricultural value of variety mixtures lies potentially in the added protection of susceptible varieties – which often appeal to growers because of specific agronomic characters – and in the exploitation of otherwise vulnerable resistance.

While random mixtures may not be a generally useful option for the ware potato sector there are certain niches where they can be used, for example, for starch production. As starch potatoes are generally late maturing and more resistant varieties, and because mixtures work best if epidemic pressure is rather low, the benefits of mixtures for the starch sector should be considerable. Depending on the mixtures used, it has been shown that significant disease reductions as well as yield benefits can be achieved.

Fresh market potatoes are grown in mixtures in some traditional systems and mixtures of different coloured potatoes may be of interest for small-scale producers. In general, however, producing different varieties in alternating rows or strips of varieties will be easier. For larger scale production, the concept of strip intercropping will be most practicable. It should reduce initial infections and the spread of disease among strips.

Scientific Developments

The lack of specific resistances in current varieties, the relatively large single plant size and the large lesion size will limit the usefulness of induced resistance, barrier effects and dilution of susceptibles in potato variety mixtures. Nonetheless, in the 1990s, research started into the use of diversification strategies in potato cropping systems especially to reduce late blight in low-input farming systems including organic agriculture, and yielded some promising and some not so straightforward results. Research has been conducted in cultivar mixtures, alternating rows, and strip intercropping. As a by-product, the effects of planting density or plant density in a region were also considered. Within agriculturally relevant limits, there is no evidence for any influence of planting density on potato late blight so that the mechanisms operating in the prevention of late blight in diversified systems cannot be augmented in this way. In contrast, the regional plant density may play a role as was shown by modelling studies and suggested by the results from different plot sizes.

To test the value of potato mixed cultivar systems in reducing late blight, several research projects were carried out with varieties with contrasting levels of resistance used in plots of different sizes. In most studies, the area under the disease progress curve (AUDPC) for the susceptible cultivar was moderately reduced (ranging from 0 to 20%) when grown in a mixture as compared to its pure stands in the absence of fungicides. However, where quantitative race-non-specific resistances were used, disease severity on the more resistant variety in the mixtures was often higher in the mixtures. This was probably due to the higher inoculum pressure on the more resistant variety when mixed with a more susceptible variety than when grown alone. Similar results were obtained when growing alternating rows or strips of differentially susceptible cultivars.

Some combinations of varieties do better in mixtures than others (‘ecological combining ability’) due to plant-plant interactions as well as plant-pathogen interactions. Furthermore, research showed that cultivars with positive general ecological combining ability are characterised by strong intra-cultivar competition in pure stands. Increases in yield between 5 and 10% have been frequently recorded in potato variety mixtures. This can lead to a design of potato variety mixtures that, on the one hand, have improved yield of the resistant varieties by reducing the negative effects of intra-cultivar competition and on the other, have improved yield of the susceptible varieties through reduced disease incidence due to the presence of the resistant varieties. Such diversification strategies are a way to reduce the inputs needed in large-scale monocultures of potatoes. Alternating rows of susceptible and resistant cultivars would be more acceptable for commercial use, but this increases the genotype unit area which reduces mixture efficiency particularly when disease pressure is high.

Plot size of individual varieties or mixtures was found to affect blight severity in several experiments. Disease may start from infected tubers or from outside inoculum. With increasing plot size the number of seed tuber borne infections will increase and so does the probability that air-borne spores will land in a plot. Larger plots had a greater AUDPC due to an earlier epidemic start, but the average rate of disease progress was greater in smaller plots. This may be because, in the smaller plots, most disease progress took place later, under more conducive conditions.

Another aspect determining the performance of cultivar mixtures is the type of resistance in the different components. Race non-specific late blight resistance is linked genetically to late maturity. This is an agronomic problem as the varieties to be mixed should be agronomically compatible, especially in maturity class. However, the largest epidemiological effects of diversification are in simple mixtures of an immune and susceptible type, or where the varieties are differentially susceptible, based on functioning major gene resistances. Race-specific resistance is not linked to maturity class. Therefore, to slow down late blight epidemics, potato variety mixtures should diversify race non-specific resistances as far as possible and also diversify for major gene resistances for which matching virulence is rare.

The question is still open whether there is a proportional response to reducing the genotype unit area (GUA) in mixtures incorporating rate-reducing resistance. However, results indicate that the benefits of improving the autoinfection: alloinfection ratio by reducing the GUA are dependent on the resistance level and type of the more resistant genotypes. The performance of some mixtures could improve at larger GUAs, as the negative impact of spores on the more resistant variety will be reduced. This implies that there is an optimal GUA, dependent on the level and type of resistance being diversified and the dispersal characteristics of the pathogen. If race-specific variation is important in the mixture effect, and the pathogen population is a mixture of simple races, then the usual arguments imply that the most intimate mixture will give the greatest effect.

It is assumed that lesser amounts of outside inoculum generally improve the efficacy of mixtures against late blight which means that part of the mixture effect might be due to differences in the spatio-temporal pattern of disease spread. A more detailed statistical analysis of spatial disease progress in different plots to test the effects of crop geometry on the incidence and severity of disease should therefore be included.

Because of the limited differences in specific resistances among current varieties and the practical problems associated with the management of variety mixtures or alternating rows, strip intercropping presents an interesting alternative especially in areas where the wind direction during the relevant times for late blight development is relatively constant. Thus, it has been shown that growing potato strips (e.g., 8 to 16 rows wide) perpendicular to the prevailing wind direction and separated by non-hosts (e.g. cereals or grass-clover) can reduce disease pressure (measured as AUDPC) by 5–23%. Such strip intercropping is equivalent to growing susceptible potatoes in strips alternating with totally resistant ones which has been modelled theoretically. Geostatistical analyses of the field experiments revealed that interference among plots within the prevailing wind direction became negligible at 20 m. Thus, when using strips, it will be most useful to separate them by at least 15 to 20 m. The analyses also showed that it is very important to consider the prevailing wind direction and that they may provide realistic estimates for the dispersal variables to be used in theoretical models.

While strip intercropping may not reduce disease to the point where it is no longer a problem, reducing disease pressure will enhance the effects of other control measures. Thus, in organic on-farm experiments, copper applications resulted in higher disease reductions in 16 to 20 m wide strips than in normal fields when tested on-farm.

An important consideration in the strategic planning of potato growing systems is the possibility to reduce the rate of adaptation of *P. infestans*. Isolates collected from two different varieties grown in strips could attack both varieties in the laboratory but they showed differences in aggressiveness due to the host of origin. These results indicate that adaptation to different potato varieties in the field may indeed take place when the varieties are grown separately. In mixtures and alternating rows inoculum interchange between cultivars may lead to a homogenisation of *P. infestans* populations leading to less cultivar-specific adaptation processes. In contrast, intercropping of potatoes with strips of different potato cultivars interspersed with other crops might result in population subdivision and allow for disruptive selection among *P. infestans* populations. There are differences in these processes between regions of high and low production intensity of potatoes. Especially where the production intensity is low it appears that strips of different potatoes generate their own *P. infestans* populations. This will contribute to disruptive selection within a season reducing the overall selective pressure for adaptation to any given type of resistance while improving, potentially, the effectiveness of the strip cropping.

Overall, diversification may be a strategy that could contribute to improved potato late blight management in organic and low-input farming systems but also under certain conditions in conventional systems. Which strategy will be most useful will depend on the type of varieties used and the final use of the crop. The efficiency of cultivar mixtures depends on the availability of several cultivars with high levels of resistance. This approach is therefore likely to be most useful in industrial starch potato production where separation of the components at harvest would not be required. Strips of different potato cultivars intercropped with non-potatoes may be an option for growers who are interested in reaping the overall beneficial effects of a more diverse farming system by reducing field sizes. With respect to the evolution and adaptive processes in pathogen populations, strip intercropping with non-potato crops may be a way to avoid the homogenisation of the pathogen populations with respect to aggressiveness towards different cultivars.

Further Reading

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