BREEDING FOR RESISTANCE IN CEREALS TO DISEASES CAUSED BY FUNGI

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Summary

Control of certain of the more highly specialized fungal pathogens of cereals has usually been attempted by breeding resistant varieties. The use of resistance controlled by single major genes has left those varieties liable to epidemic attack by new virulent races of the pathogens. Alternative ways of using major gene resistance are discussed and recent work on attempts to breed varieties with non-race specific resistance considered.

INTRODUCTION

CEREAL CROPS of the present day are subject to infection by a wide range of fungal parasites, each with its own characteristic mode of attack, effect on the plant, and potential for adversely influencing the crop's performance in the field. At one extreme of the range of cereal diseases are the facultative parasites characterized by the soil-inhabiting *Pythium* and *Fusarilum* root-rotting fungi, which are chronic, show little or no race differentiation, and for which the most effective means of control are crop rotation and chemical treatment of the seed rather than by breeding for resistance. On the other hand, some of the disease-causing organisms are obligate parasites on cereals, and may have marked differentiation into pathologic races. These fungi can induce disease epidemics under conditions favourable to them and for which the production of resistant varieties by plant breeding techniques is the most effective control. Cereal powdery mildew and leaf and stem rust are good examples of these sophisticated parasites and they will serve as the principal examples of disease resistance breeding in this paper. Between the two extremes of disease-inducing fungi already mentioned exist a wide range of intermediate forms with their own particular spectrum of characteristics.

THE INFLUENCE OF PLANT BREEDING ON THE HOST-PATHOGEN RELATIONSHIP

Prior to the advent of scientifically based cereal-breeding, a balance must have been established between the host crop plant and the pathogenic fungus in which the genetic heterogeneity of the host protected the crop from massive attack, but also enabled the pathogen to persist.

Cereal breeding in the 20th century has, however, dramatically changed this balance. Its initial effect has been to increase substantially the genetic uniformity of the crop caused by the selection and propagation of the best components from the previously very mixed varieties. Many of these selected stocks would still possess a genetically broadly-based resistance to diseases as carry-over from the primitive host-parasite relationship. This is "horizontal resistance" in the terminology of Van der Plank (1963, 1968), which has also been termed "generalized resistance" in a recent paper by Smith and Smith (1970).

The breeding for disease resistance in cereals really had its roots in the observations of Biffen (1905) who demonstrated that resistance to yellow rust in wheat was controlled by a single genetic factor. This led to a substantial effort in many countries for the breeding of simply inherited resistance to cereal diseases and is still the basis of much of this work carried out today. For resistance to the cereal rusts, genes in the host which gave a hypersensitive reaction—*i.e.*, the isolation and elimination of the infection by rapid host-cell death giving a necrotic fleck reaction—were extensively used, giving "vertical resistance" in the nomenclature of Van der Plank.

The extensive cultivation of varieties with this simply-inherited type of resistance led to a change in the host-pathogen relationship to an intimate genetical correspondence in delicate balance. Any physiological race of the rust-fungi that had the capacity to attack a widespread variety with a single gene for resistance enjoyed a considerable selective advantage over others and it was subsequently established that this capacity to attack was itself conditioned by a single gene for virulence in the pathogen. Consequently a "gene for gene" relationship became established between the host and its parasite and changes in the genetical constitution of the resistance in the host by the introduction of a new resistant variety generally led to a change in the spectrum of genes for virulence in the pathogen. New factors or combinations able to attack that variety arose by mutation or genetical recombination and became predominant.

Further implications of this method of plant breeding are manifest in the "Vertifolia effect" named after a potato variety which showed extreme susceptibility to new races of potato blight. In the rigorous selection for major gene resistance to disease which could be readily identified by specific host reaction to certain races of the pathogen, a dilution by genetical recombination of the factors for the horizontal resistance principally exhibited by the older varieties and upon which selection pressure could not be exerted undoubtedly occurred. As a consequence, some varieties in which the major gene resistance was no longer effective because of the development of new rust races lacked any residual disease resistance to impede the development of a disease epidemic. The fact that single gene rust resistance is frequently transient led to catastrophic epidemics of stem rust on wheat in North America in the years 1935, 1953 and 1954.

In New Zealand the best example of the unsuccessful use of vertical resistance is the work on powdery mildew resistance in wheat started at the Wheat Research Institute in 1946. This work was continued in a backcrossing programme at the Crop Research Division and culminated in the release in 1961 of the two varieties Hilgendorf-61 and Cross 7-61. By 1964, however, their resistance had completely broken down and a parallel programme to develop an Aotea line with vertical resistance was then abandoned (Copp, 1964; Vizer, 1964).

This experience with wheat powdery mildew, however, was not typical of several other successful projects in New Zealand where permanent resistance to plant diseases had been achieved using vertical resistance. Some examples of these were resistance to flax wilt, pea wilt and tomato wilt, (all caused by strains of *Fusarium oxysporum*) potato viruses X and Y, and pea mosaic virus. In all these cases new pathogenic biotypes of the pathogen have been described at various times but they have lacked the ability to adapt for survival or to compete in the field environment where the disease has been of economic importance. Apart from these examples of successful breeding for "vertical resistance" there were numerous other examples where, because of the lack of monogenic or simple resistance factors, plant breeders had worked on "horizontal resistance" and achieved both a satisfactory level of resistance and performance in action. Typical examples of the use of horizontal resistance in the New Zealand scene are powdery mildew resistance in Dreadnought, Arawa and Fife-Tuscan wheat varieties and more recently with barley yellow dwarf virus resistance in the Mapua and Amuri oat varieties and Research barley. Poha, a pea variety combines vertical resistance to Fusarium wilt and pea mosaic with horizontal resistance to pea leaf roll virus.

BREEDING TECHNIQUES FOR DISEASE RESISTANCE IN CEREALS

It has already been pointed out that the use of vertical or major gene resistance, which has by and large controlled epidemics, has had associated with it some unfortunate side-effects. A further problem has arisen in the need to have available a regular supply of effective genetic factors for disease resistance and the fear has been expressed that the supply may be ultimately exhausted. The search for new genes has been extended to species allied to wheat.

A further refinement in using this type of resistance has been to group the factors together in pairs or even more complex aggregations within a single genotype to protect the variety against susceptibility to a single mutation for virulence in the pathogen, cross-protection from the other factors for resistance being obtained. However, genetical recombination is a potent force in the re-assorting of genes for virulence in the pathogen and new races have continued to appear to attack the resistance complexes.

An alternative way to use the major genes has been in the establishment of multilines in which a genetical diversity for disease resistance in the variety is obtained without loss of uniformity for other characters. This is obtained by breeding a series of backcross derivatives of a single variety, each derivative differing in its gene or genes for disease resistance but being similar to the recurrent variety in other features. A mixture of these lines in the field gives a variety of acceptable agronomic uniformity but, by virtue of the variation from plant to plant in disease resistance, dilutes and reduces the attack of specific races and thus slows the build-up of disease epidemics.

The widespread growing of this type of variety could result in the stabilization of the pathologic races. This approach has not yet been extensively used although it has been intensively investigated since 1961 in North America.

As an alternative to disease resistance based on major genes, there has recently been much interest in a return to the use of horizontal or non-race-specific resistance that was probably an important component in the disease resistance of older varieties. This resistance, once established in a variety, should be long lasting and proof from changes within the pathogen population, a most desirable attribute.

The techniques of detecting horizontal (generalized) resistance have been examined for several years at DSIR, Lincoln, and the methods for wheat powdery mildew described by Smith and Smith (1970). These studies have shown that it is generally very difficult to detect the really valuable differences in adult plant reaction to disease at an early stage in plant growth. For example, wheat seedlings up to about 4 weeks of age showed very slight differences in susceptibility between the wheat varieties Dreadnought, Arawa and Aotea. They were all severely affected. However, after shooting, at Feekes stage 10.2, there were highly significant differences which could be readily identified by sampling four uppermost leaves of at least six tillers of each variety. In glasshouse trials, it was established that these differences in adult plant reaction to mildew accounted for the major yield effects from this disease. For example, under the most severe level of mildew infection, the yield reduction for Aotea was 50%, for Arawa 20%, and for Dreadnought 10%.

Surveys of mildew incidence in the field near Lincoln in recent years indicated that, under severe infection levels in Aotea, the yield loss was about 30% but that the average yield reduction over the country was less than 10% of the yield for the most susceptible varieties Aotea and Hilgendorf 61. Varieties such as Dreadnought suffered less than 0.1% and the commonly grown variety Arawa suffered less than 1% loss in yield. It is suggested that this level of horizontal resistance present in the variety Arawa gave an adequate and certainly a permanent level of resistance under New Zealand conditions. Studies on the new variety Kopara and various reselections of this variety have shown that it had a level of horizontal resistance slightly inferior to Arawa but still adequate under the current level of fertility for wheat growing in New Zealand.

Breeding to select an Aotea and a Hilgendorf type wheat variety with the "Arawa" level of horizontal resistance has been in progress since 1965 and promising lines are under field evaluation this season.

With barley yellow dwarf virus, breeding for horizontal resistance in wheat, oats and barley has been complicated by the difficulty of obtaining a reliable index of relative susceptibility. The only really reliable index has been the grain yield and the main obvious limitation of this index is that it is obtained too late to enable the selections to be used immediately in a crossing programme. This difficulty, however, is not insurmountable as can be seen by the success in breeding horizontal resistance to pea leaf roll virus in Poha pea and barley yellow dwarf virus in Mapua oats.

Many groups are investigating the potential of horizontal resistance for establishing lasting resistance to a number of diseases in cereal crops and many plant breeders are re-evaluating their methods of breeding for disease resistance.

Taken in perspective, however, it is apparent that both with vertical and horizontal resistance there is scope to obtain adequate levels of permanent resistance to the main diseases of cereal crops and that therapeutants will provide a temporary expensive control for the more obstinate disease.

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