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The Ecology and Genetics of Host-Pathogen Relationships in Wheat Rusts in Australia

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Investigations concerning the host-parasite relationships in wheat rusts directed towards the ultimate control of these diseases, have been in progress in Australia for almost 50 years. Although it was at first thought that such an undertaking would be relatively simple, it soon became clear that there was insufficient basic information on (a) the extent of the variability in the fungi involved, and (b) the genetic nature of the resistance to them. Information accumulated on these two aspects of the problem has greatly facilitated progress in the control programme.

HOST GENOTYPE IN RELATION TO GENES FOR VIRULENCE

Since the Australia-New Zealand area is isolated geographically from other countries where wheat is grown, there has been a unique opportunity to observe the evolution in the field of those pathogenic strains of rust which are best adapted to the climatic conditions of the area and to the medium for growth offered to them by the commercial crop of the time. These strains, which we can presume to have arisen and evolved locally, are thus unaffected by the physical or biological environment prevailing elsewhere. This is a situation in marked contrast with that on both the north and south American continents where strains originating in one may be transported as spores to another. Moreover, the variation in the leaf rust and in the stem rust organisms has arisen regardless of the virtual absence of the alternate hosts *Thalictrum* spp. and *Berberis* spp., respectively.

The period of investigation from about 1920 to 1942 was characterised by a predominance of strains which were present prior to the commencement of any wheat breeding programme to control them. Since 1942, however, the frequencies of certain genes for virulence in the fungal population have been influenced by the frequencies of the corresponding host genes for resistance in the wheats grown commercially. Although five hosts genes, *Sr6*, *Sr11*, *Sr9b*, *Sr9c* (unpublished) and *sr17*, have been involved only two of them will be discussed in detail.

Sr6

Eureka, a cultivar released in 1938, represented the first popular stem rust resistant wheat originating from a breeding programme in Australia. When released it was highly resistant to all strains recorded in the country, the most prevalent at that time is now designated 126-6,7 (culture 334). After four years of cultivation a new strain 126-1,6,7 (culture 7316) was isolated and, since it differed from the putative parent only by virulence on seedlings having the gene *Sr6*, it is presumed to have arisen from it by mutation. The subsequent developments in this relationship between host and pathogen have been traced by WATSON (1958) and by WATSON and LUIG (1963). It will be clear from the earlier work and from the distributions presented in Figure 1 that Eureka has had two periods of popularity. In the first it reached its peak in the mid 1940's, and in the second the highest acreage was in 1963. With the declining frequency of the gene for virulence on plants with *Sr6* which ended in the failure in 1960 and 1961 to recover any strain having such a gene, Eureka again emerged as a resistant, high yielding cultivar. It was again recommended to growers, partly because of its fine agronomic performance, and partly to give an opportunity to observe the effect of such a reintroduction on the stem rust flora. Strain 126-1,6,7 had disappeared and the standard races 21 and 34 had replaced 126 and 222. As already reported (WATSON and LUIG, 1963) the result was that a new series of strains developed each having a gene for virulence on plants with *Sr6*. The farmers recognised the renewed susceptibility of Eureka, its popularity declined and the experiment demonstrated that evolution in the organism was proceeding in a forward direction without the resurgence of old pre-existing strains.

Sr11

When Eureka first became susceptible in 1942 a series of new cultivars with the gene *Sr11* were released. Gabo, Charter, Kendee and Yalta were among the common ones and the acreage sown to them increased dramatically (Fig. 1). The parallelism between virulence gene frequency and corresponding resistance gene frequency is not as close as in the case of *Sr6* but the discrepancies for the period 1955-1957 have already been explained (WATSON, 1958).

The fall in the frequency of the gene *Sr11* in the population over the past 10 years has been due to the replacement in northern N.S.W. and Queensland of cultivars such as Gabo (*Sr11*) by Gamenya and Festival (*Sr9b*), Spica (*sr17*) and Mengavi (*Sr9c*). The virulence gene in the rust, corresponding to *Sr11* was present in 95 per cent of the isolates in 1958 but in only 45 per cent in 1966. These results again highlight the close relationship between host and fungal genes, however, there has been some interference to the general pattern by the occurrence of strain 21-4,5 which is virulent on seedlings with both *Sr9c* and *sr17* but avirulent on those with *Sr11*. Moreover, Figure 1 shows a recent rise in both the frequency of *Sr11* and of the corresponding virulence gene. The former is attributable to the cultivation of Mendos (*Sr11 Sr9c sr17*) and Gamut

(*Sr6 Sr11 Sr9b SrGt*, unpublished), but the latter is not due to the increase of strains virulent on them. It is attributable to a reduction of the frequency of strains such as 21-4,5 and an increase to 21-2,3,7. The latter thrives on Gamenya which is still a popular variety and, although virulence on plants with *Sr11* is not necessary, this strain has a high survival value.

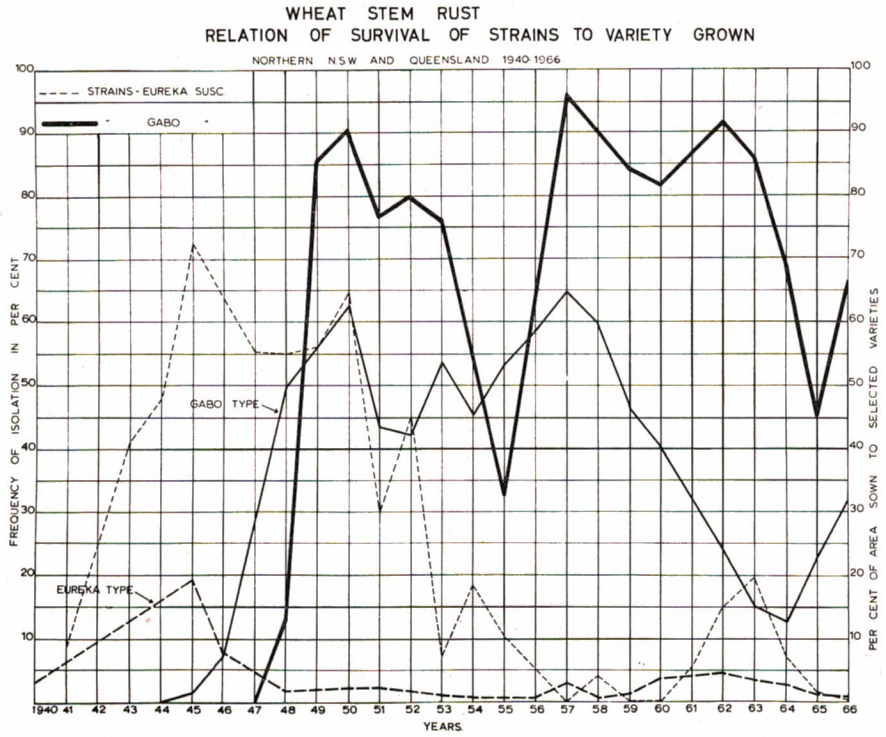

FIG. 1. The relationship between the percentages of the acreage sown to cultivars with the genes *Sr6* and *Sr11* in northern N.S.W. and the percentage frequency of the strains of rust attacking them in northern N.S.W. and Queensland.

The results of these tests with *Sr6* and *Sr11* suggest two things. The first is that where cultivars have a simple genetic mechanism for resistance such as Eureka, temporary withdrawal from cultivation will have little value for control; and the second is that certain strains such as 21-2,3,7 may predominate with more than the minimum number of virulence genes necessary for survival.

RELATION OF FUNGAL SURVIVAL TO ACCUMULATION OF VIRULENCE GENES

Previous field studies under Australian conditions suggested that when grown on susceptible cultivars, there may be a negative correlation between the survival ability of a rust strain and the number of specialised genes for

virulence which it possessed (WATSON, 1958). Indeed, FLOR (1956) has suggested that genes for virulence, not necessary for survival under natural conditions, may be lost. Few laboratory experiments have been conducted to test the validity of this general supposition which is based largely on results from field surveys. For example, strains of the leaf rust organism which were prevalent in New Zealand in the early 1920's still predominate there. No concentrated effort has been directed towards controlling them by breeding in that country, but the same strains, which were once also prevalent in Australia, have been eliminated by the use of resistant cultivars. Those leaf rust strains which have evolved here since breeding work began have, of necessity, accumulated more genes for virulence, but, despite their aerial transportation, they have been unable to establish themselves in New Zealand on cultivars which are equally susceptible to them and to the earlier strains.

One of the most recent studies on differential survival has been carried out by KEED (unpublished), who grew strains of stem rust in pairs in the glasshouse on host plants which were equally susceptible to both strains. The strains she used varied in their range of virulence on host seedlings having one of the following genes, *Sr6, Sr11, Sr9b,* or *Sr15.* Figure 2 is representative of the results obtained in a series of such studies. Strain 21-1,2,3,7, which is widely virulent (viz. virulent on seedlings having all four of the above-mentioned genes in combination) was mixed in three different initial amounts with strain 21-7 which is narrowly virulent (viz. virulent on seedlings with *Sr15* alone, but avirulent on all other combinations of above host genes). The mixture was continued in duplicate through successive uredial generations and analysed by inoculating seedlings having the gene *Sr11.* Regardless of the initial proportion of the two components in the mixture strain 21-1,2,3,7 predominated after four generations. In other combinations this same strain overran the component with which it was associated.

Strain 21-1,2,3,7 occurs in the field in eastern Australia and with strains identical in designation with those studied by KEED. On the basis of her results on seedlings in the glasshouse, it could be expected that this strain would predominate in the field. This has not been the case and at this point the field and laboratory results are in conflict. There would be many factors to consider should one attempt to simulate field conditions in the laboratory, and the disagreement may be attributable to the different environments in the two situations. On the other hand, KEED worked with seedlings rather than adult plants and with pure cultures which may not be typical of the strains they represent; inconsistencies could thus occur from culture to culture depending on the genotype.

From these results obtained by KEED it is impossible to support the proposition suggested by FLOR, and more work is required. Should strain 21-1,2,3,7 become prevalent in the field in the meantime, it is possible that variation and selection for aggressiveness will occur, and thus the genes for virulence and survival may be combined.

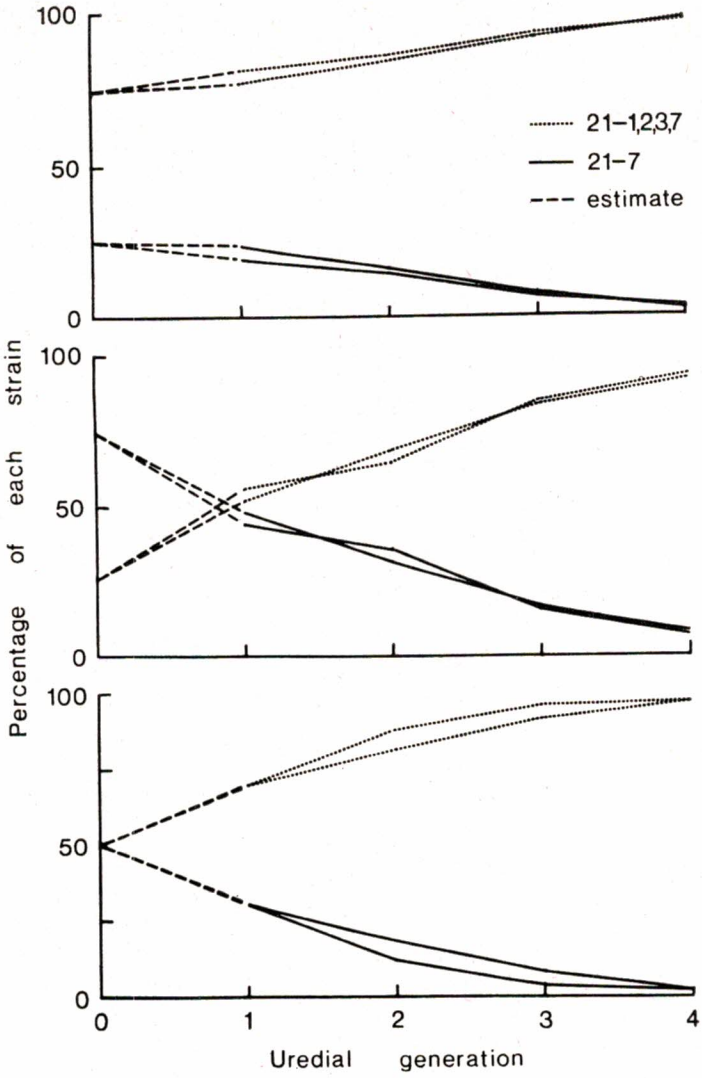

FIG. 2. Percentage survival of two strains of stem rust when mixed in three different proportions and grown on a host equally susceptible to both.

ORIGIN OF THE NEW STRAINS

It is now well known that variation for pathogenicity in wheat rusts may arise as follows:

1. sexually on the alternate host
2. asexually on the graminaceous host by
   - A. mutation
   - B. somatic hybridisation
     - (i) nuclear exchange
     - (ii) some other process.

Species of barberry (*Berberis*), the alternate host of *Puccinia graminis tritici* occur in the Australia-New Zealand area but they have only been found infected by rust in Tasmania and in one isolated area in New South Wales. Thus sexual reproduction in the fungus is so rare that it cannot be invoked to explain the variation in pathogenicity that occurs over a widespread area including Western Australia, eastern Australia and New Zealand. The organism may live from one season to another in all these areas on volunteer wheat and barley, as well as on annual and perennial grasses. *Puccinia graminis secalis* commonly occurs on rye (*Secale cereale*) but it may also occur along with *P. graminis tritici* on barley and several of the above-mentioned grasses. Under these circumstances there is ample opportunity for asexual variation to occur at any time of the year.

We have already outlined (Watson and Luig, 1963) the field circumstances surrounding the origin of strain 34-2,4, from 34-2 presumably by mutation, and in 1964 we isolated strain 34-2,4,5 in an almost identical situation except that Mendos (*Sr11 Sr9c sr17*) was the screening cultivar, rather than Mengavi (*Sr9c*). Since both forward and back mutation have been recognised in the laboratory (Luig, 1967) this process is foremost among those involved in asexual variation in Australia.

Mutations of the type described are highly specific and involve a sudden change in the pathogenicity of one host-pathogen complementary system. However, recently we have gained preliminary information to suggest that all changes may not be of this type (Watson and Luig, 1968). These data showed that the change from avirulence to virulence may proceed in stages, but, whatever the nature of the changes in the fungus may be, the same gene in the host controls the resistance to the original strain and to the intermediate variants of it. Both genes *Sr6* and *Sr11* were shown to be involved in this kind of variation.

We have demonstrated that somatic hybridisation takes place between strains of *P. graminis tritici* as well as between the appropriate strains of *P. graminis tritici* and *P. graminis secalis* when these latter are growing on the same plants. Recent evidence suggests that at least some of the variability we have observed in the field can be attributed to asexual hybrids between them on the common host *Agropyron scabrum* which is widespread and regularly infected by both in Queensland.

Compatibility between *P. graminis tritici* and *P. graminis secalis* is also evident in that they can be readily hybridised on the alternate host. However, the progeny from sexual and asexual inter-crosses are mostly non-pathogenic on common wheat, presumably because they have inherited from *P. graminis secalis* many dominant genes for avirulence on this host. The evidence from several experiments suggests to us that *P. graminis tritici* and *P. graminis secalis* are differentiated by a number of genes for virulence. If this is so, we can assume on the basis of the gene for gene concept that wheat and rye are resistant to the reciprocal rusts by virtue of the operation of genes for resistance in the host and genes for avirulence in the fungus.

The following results support this interpretation.

1. Rye, a heterozygous outbreeding species, will, on inbreeding, give progenies which are fully susceptible to strains of *P. graminis tritici.* The cultivar Black Winter Rye comprises less than 2 per cent of plants susceptible to wheat rust. From these latter, line 5 (TABLE 1), which is fully susceptible to strains of both *P. graminis tritici* and *P. graminis secalis,* has been derived.

2. By inbreeding *P. graminis secalis* and selecting the progeny on wheat genotypes, it has been possible to remove many of the dominant genes for avirulence from *P. graminis secalis.* The cultures listed in TABLE 1 as H34 and A20 are the sexual progenies from the original culture 57241.

3. By selecting lines of *P. graminis secalis* from the alternate host, it should be possible to observe some which have more genes for avirulence on wheat than those represented in a typical field isolate of this rust. This has been done in the selection of culture 67401 (TABLE 1) from barberries under natural conditions, but the source of the original teleutospores is not known with certainty.

4. From the intercrossing of wheats which have no major genes for resistance to *P. graminis tritici* but which are resistant to *P. graminis secalis,* it has been possible to derive hexaploid wheat almost completely susceptible to the standard culture of *P. graminis secalis,* 57241. The reactions of one such line, W2691, are given in TABLE 1 but it is clear that genes still remain for resistance to culture 67401. Some of these genes have been removed by intercrossing W2691 with other genotypes.

5. Various stocks selected from the genus *Triticum* have become useful in the identification of a series of strains of *P. graminis secalis* as well as for the separation of probable hybrids between it and *P. graminis tritici.*

Three groups of strains have been listed in TABLE 1. The first group has a concentration of genes for virulence on wheat, but they are avirulent on unselected Black Winter Rye. The third group has mostly genes for avirulence on wheat but for virulence on rye. Of course, not all cultivars of rye will be susceptible to this group of strains. The second group of strains comprises the supposed asexual intercrosses between strains of the other two groups. Wheats such as Purple Straw, Brevit and Vernal Emmer clearly differentiate the intercrosses suggesting that there has been a recombination of genes for avirulence and virulence in these strains following hybridisation. From wheat cultivars typical of those in TABLE 1, SANGHI (1968) has isolated several previously undescribed genes for resistance to *P. graminis secalis* and to hybrids between it and *P. graminis tritici.*

GENETICS OF RESISTANCE IN RELATION TO BREEDING

A knowledge of the ecology of the rust fungi and of the genetic nature of their virulence is important in a breeding programme, but of greater importance is a knowledge of the genetic nature of the type of resistance being utilised.

TABLE 1. Infection types produced on 8 wheats and on Black Winter Rye by strains of *Puccinia graminis tritici*, *Puccinica graminis secalis* and probable asexual intercrosses between them.

Host	STRAINS										
	P. graminis tritici			Probable Intercrosses					*P. graminis secalis*		
	116-4,5	21-2,7	21,7	67178	67177	67222	67149	H34	A20	57241	67401
Marquis	3+	3+	3+	;1	2-,3	x—	;	;	;	;	;
Brevit	3+	3+	3+	2+,3	2	;2=	3	;	;	;	;
Norka	X+	3+	3+	2+,3[c]	;	;1	;1	0;	0;	0;	0;
Vernal Emmer	3+	;2=	;2=	;	3	;	;	0	0	0	0
Purple Straw	3+	3+	3+	2—	3+	3+	;2=	;2	;2	;2	;
Little Club	3+	3+	3+	2+,3	2=	2+	;2=	3+	2—	2—	;
W2691	3+	3+	3+	3+	2+,3	3	2,3	3+	x+,3	2,x+	0;
Yalta	;2=	3+	;2=	;	;	;2=	;	;	x,3[c]	;1—	0
B.W.R.	Seg.*	Seg.*	Seg.*	Seg.**	2+,3	Seg.**	Seg.**	3+	3+	3+	3+
B.W.R. line 5	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+

* Usually 1-2 per cent of the plants give 3 reaction.
**Usually 60-65 per cent of the plants give 3 reaction.

Mention will be made of only two categories, *viz.*, Specific Resistance and Non-Specific Resistance. Our studies have been mainly concerned with the former.

1. Specific Resistance

(A) *Resistance operating throughout the life of the plant.*

(i) Simple genetic systems. Wheat plants which carry certain of the well-recognised major genes such as *Sr6* and *Sr11* are resistant both as seedlings and adult plants provided the same strain is used and the conditions of temperature and light are the same at both stages of growth. There may be an interaction between host, pathogen and environment so that seedlings resistant to a particular strain at one temperature, are susceptible at another. The host-pathogen relationship is very specific and the gene in the host concerned in resistance may have originated in different ways.

(a) From genotypes within hexaploid species of *Triticum*. Most of the genes currently used in breeding work have been derived from a genotype readily crossable with *T. aestivum*. The genes *Sr6*, *Sr11* and *Sr9b* belong in this category. When present singly in a commercial cultivar they have been rather short-lived in their usefulness for the control of rust.

(b) From genotypes within tetraploid species of *Triticum*. Many different types of specific resistance were originally present in wheats belonging to the tetraploid group. The genes have been transferred to the hexaploid parents by conventional interspecific hybridisation as the tetraploid types were believed to carry a resistance more valuable than that in the hexaploids. *Sr11* was transferred from Gaza at a time when it was not known that the same gene was present in lines of hexaploid wheats from Kenya. Khapstein was developed from Khapli Emmer since the latter had resistance to many strains throughout the world. While *Sr11* from Gaza has not been particularly valuable, *Sr13* from Khapli is still rather untested as it has not yet been incorporated into a commercial cultivar. The gene *sr17* has been transferred from the cross Marquis x Yaroslav Emmer, and although seedlings having this gene are highly resistant against specific strains in Australia, so far no rust culture from the United States has been found which possesses a gene interacting with *sr17*. The gene *Sr9c* which has been transferred from *T. timopheevi* to Timvera and to C.I.12632 and C.I.12633 is present in the cultivars Mengavi and Mendos. It is concerned in a highly specific interaction and strains such as 21-4,5, 21-2,4,5, 34-2,4 and 34-2,4,5 are variants which have the gene for virulence corresponding with *Sr9c*. To these latter strains, however, the original parent *T. timopheevi* is highly resistant. Studies are in progress to transfer the gene(s) responsible to a hexaploid wheat for use in future breeding work.

In a study by Khan (1960) a major gene from *T. durum* was transferred to hexaploid wheat. An analysis of seedlings having it has shown that the

gene concerned in the reaction is identical with that in Vernal Emmer. A derivative of this has been named Vernstein (LUIG and WATSON, 1967). It is anticipated that this gene will be utilised in providing further genetic diversity in the breeding programme.

(c) From genotypes within diploid species of *Triticum*. The only diploid species so far tested to any extent is *T. monococcum*. This has differentiated many of the standard races present in the country and seedlings are fully susceptible to standard race 17. However, as with the gene from Vernal Emmer it could provide further genetic diversity.

(d) Genes from genera other than *Triticum*. These have been used in a limited way. Material having a resistance from *Agropyron* has been made available by KNOTT (1961) and, although not yet incorporated into a cultivated wheat, the gene responsible has been shown to be effective against all strains of stem rust so far recognised in Australia. Resistance from *Secale* is also available but except for certain pathological studies this resistance has not been used in breeding. The use of genes from *Secale* presents a somewhat different problem from that with *Agropyron* since there is a well-established fungus, *P. graminis secalis*, which attacks *Secale* plants.

When a gene for resistance to *P. graminis tritici* from *Secale* is transferred to *T. aestivum* the line carrying it will also be resistant to *P. graminis secalis* because of the genes in the *T. aestivum* background. However, certain hybrids between *P. graminis tritici* and *P. graminis secalis* may be pathogenic on such a line due to a combination of virulence genes from both varieties of *P. graminis*. On the other hand, our results show that certain well known genes for resistance to *P. graminis tritici* such as *Sr11* are ineffective against *P. graminis secalis* (TABLE 2).

TABLE 2. Reaction of seedlings of lines backcrossed to W2691 and having the genes *Sr6* and *Sr11*, when tested with strains 126-6,7 (culture 334) of *P. graminis tritici* and culture 57241 of *P. graminis secalis* at temperatures of 65° – 70° F.

	126-6,7	57241
W2691	3+	2+,3
BC Line with *Sr6*	;1+	2,x+
BC Line with *Sr11*	;2=	2+,3
Black Winter Rye	;	3+

(e) Combined genetic systems. In our breeding programmes progress has been made by successively adding genes to agronomically well adapted genotypes as new rust strains arrive which make possible the recognition of these genes. Plants so derived have a broad genetic base and can be expected to protect the plant against many strains and also to have a more stable resistance. There is still no data to support the second of these expectations but such

a broad base would be highly effective when parental material is examined on a world-wide basis.

In this connection, RAJA RAM (unpublished) selected eight parents, including six from the 1963 International Rust Nursery, each of the latter having a low average coefficient of infection to stem rust. All eight parents were found to have more than one gene for resistance. In addition to the well recognised genes, several hitherto undescribed were isolated. As many as six genes were detected and studied in certain of the parents. These genes were mostly specific and operated in seedlings, others were effective only in adult plants.

(B) *Resistance operating only in the adult plant stage.*

Several stocks of wheat are known in which the genetic nature of the resistance to rust is simple but the genes concerned do not operate until the plant is at an advanced stage of growth. Notable among these are Chinese Spring, resistant to leaf rust, and Renown which, although having the gene *sr17*, also carries another gene(s) which is concerned in a high seedling infection type but gives resistance in the adult plant. A gene, possibly the same as the latter, is also present in cultivars such as Hofed, Warigo and others derived from Hope and H-44. For some time it was considered that adult plant resistance was the type on which breeding programmes should be based but the experience in Australia would suggest that, if controlled by a simple genetic system, strains may readily develop which render this resistance also ineffective.

2. NON-SPECIFIC RESISTANCE

It is well-known that certain cultivars of wheat, although not highly resistant, are damaged less than the fully susceptible ones when a severe epiphytotic of rust develops. Little work has been done with this type of resistance in Australia, but it would appear that although it may be less effective, more subject to environmental influences, and difficult to manipulate in a breeding programme, it should be the subject of more intensive investigation. The obvious role of this resistance would be to provide a background of resistance in the cultivars of the future, to which could be added the major genes for specific reactions. One cultivar which may have value in this connection in Australia is Hopps, and studies are in progress to determine the genetic nature of this material.

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