1958 Farrer Memorial Oration . . .

The Present Status of Breeding Disease Resistant Wheats in Australia

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TO-DAY we commemorate the name of William James Farrer and it is appropriate to look briefly at the changes in varieties that have occurred during more than half a century of wheat production. Farrer worked almost single handed. Wheat breeding to-day is a national undertaking in all the wheat producing States of the Commonwealth.

Before 1900 the varieties of wheat being grown here were a nondescript group. Some had been brought from England by the early settlers, others had probably originated in shipments of wheat sent as food from South Africa. Many had no recognised names and were cultivated under a name that had been applied locally. According to Wenholz (1934) the most popular varieties about 1900 were Steinwedel, Purple Straw, Allora Spring, King's Jubilee, White Lammas, Australian Talavera, Farmers' Friend, Rattling Jack, White Tuscan, Golden, White Essex and White Hogan. Ten years later, Farrer's varieties were largely superseding those previously grown. Those cultivated most widely were Federation, Florence, Rymer, Bobs, Comeback, Bunyip, Firbank, Cleveland, Thew, Warren and Jonathan.

The influence of Farrer's varieties was so great that the area sown to them rapidly increased as the overall production of wheat in Australia expanded. Federation became the leading wheat and held that position until 1925. The remarkable characters shown by this variety have been appreciated in many wheat producing countries of the world, and even in recent times it is cultivated in the western United States (Pugsley 1953). Florence, another of Farrer's varieties which was rust escaping by virtue of its earliness, is still commercially grown in eastern Australia. The latest census shows that 179 acres were sown in Queensland in the 1956-57 season.

It was inevitable that the varieties developed by Farrer would eventually be replaced by higher yielding, better quality types; and the names of a group of breeders will always be associated with the immediate post-Farrer period. J. T. Pridham and R. J. Hurst worked in New South Wales, while H. Pye and G. S. Gordon were breeding for Victorian conditions. W. J. Spafford and R. C. Scott are well known for their work in South Australia, while Western Australia was represented by E. J. Limbourn and Queensland by R. E. Soutter. The varieties Nabawa, Ranee, Free Gallipoli and Ford are a lasting tribute to those who worked in this field prior to 1930. Over 65,000 acres of Ford were grown in New South Wales in 1956-57.

Modern varieties, which have largely resulted from the concerted effort of another group of men, show a progressive improvement over those grown earlier. Wheat breeders have kept in mind three aspects of the problem when embarking on a general improvement programme. These aspects are:—

Agronomic characters, the foremost of which is yield.

Disease resistance, particularly flag smut and to some extent stem rust.

Grain quality.

These three phases of the problem have by no means received the same emphasis in each of the states and, consequently, the acreages sown to strong and medium strong wheats are low in Victoria and Western Australia, but relatively high in South Australia, New South Wales and Queensland (Callaghan 1954). It is true that soil and climate also influence quality, but new varieties have contributed a great deal towards a general improvement in Australian wheat. According to Callaghan the percentage of strong to medium strong wheats grown throughout the Commonwealth rose from 3.3 in 1932 to 25.6 in 1952.

More work on wheat improvement is being done now than ever before in the history of the country and an even greater effort can be expected over the next ten years. The names of many people are connected with the steady increase that is evident in the yield and quality of Australian wheats, but the chief are W. L. Waterhouse, A. R. Raw, A. J. Millington, S. L. Macindoe, E. J. Breakwell, W. V. Single, A. T. Pugsley and E. C. B. Langfield.

THE FARRER MEMORIAL MEDAL is awarded annually to commemorate the work of Australia's great wheat breeder, William James Farrer, and to mark distinguished service to agricultural science. The oration by the recipient is an important item on the programme of the congress of the New South Wales Agricultural Bureau at which the award is made.

All states have made contributions in this modern era and characters of varieties have come to be associated with a particular institution. Varieties from the Victorian Department of Agriculture, for example, are characterised by a shortness of the straw and a dense head. Insignia would be typical of this group and it is a high yielding variety. Western Australian varieties, on the other hand, still undoubtedly of high yielding ability, are tall and a weakness of the straw is apparent when grown on the fertile soils of the northern zones of the eastern wheat belt.

Many different environments exist throughout the country and a great diversity of varieties adapted to these conditions have been bred. Since no restrictions have been placed on what varieties may be grown, farmers have had a wide choice for any particular locality. This has resulted from the low standards of quality that have been accepted in the past. It appears that the choice of varieties suitable for any one area is excessively wide, but as long as the farmer can sell whatever variety he grows, this situation will continue. We have now reached a stage in wheat improvement in Australia when certain varieties should no longer be accepted by the flour milling trade.

The data of Table 1 and Figure 1 show the importance of different wheat varieties grown throughout Australia and their reaction to the four diseases dealt with in the present report; namely, stinking smut, flag smut, leaf rust and stem rust. In preparing this table varieties occupying less than 50,000 acres have not been considered, and in Figure 1 only varieties sown on more than 175,000 acres in 1956-57 have been listed. While all those varieties appearing in Table 1 are relatively high yielding in their appropriate environment, it will be observed that no variety completely disease resistant is widely grown. Gabo and Wongoondy are resistant to stem rust in Western Australia, but strains of the organism occur elsewhere to which they are susceptible.

Four diseases are important in the Australian wheat belt and breeding work has been carried out against all of them. These are bunt or stinking smut, flag smut, leaf rust and stem rust. Rust diseases occur with greatest frequency in the northern wheat zones of New South Wales and Queensland. Bunt may develop in all districts. Flag smut is most severe in the lighter soils of New South Wales and the other States. It is not usually important in Queensland nor on the heavier soils of north-western New South Wales. Other diseases such as foot rots, take-all and leaf blights, may be damaging in certain seasons but no breeding work has been undertaken to control them.

The present situation with regard to problems connected with breeding varieties resistant to the four abovementioned diseases will now be considered in more detail.

BUNT OR STINKING SMUT

The name of William Farrer will always be associated with the production of bunt resistant wheats, but since the release of Florence and Genoa over fifty years ago, little progress has been made in the breeding of further bunt resistant varieties. In the years following Farrer's work, most of the wheat grown was susceptible to bunt and wet pickling in copper sulphate was used as an effective control measure. It was an

TABLE I.

Acreages and disease reactions of Australian wheat varieties cultivated on more than 50,000 acres in 1956–57

Variety	Acres	Per Cent of Total	Disease Reaction			
			Bunt	Flag Smut	Leaf Rust	Stem Rust
Gabo	1,547,018	19·0	S	S	†	*
Insignia	1,400,740	17·2	S	R	S	S
Bencubbin	965,918	11·8	S	R	S	S
Bungulla	578,445	7·1	S	R	S	S
Pinnacle	351,021	4·3	S	R	S	S
Wongoondy	276,730	3·4	S	R	S	*
Kondut	263,699	3·2	S	R	S	S
Quadrat	227,034	2·8	S	R	S	S
Glenwari	202,371	2·5	S	R	†	R
Dirk	201,409	2·4	S	R	S	S
Festival	179,185	2·2	S	R	†	R
Kendee	142,588	1·8	S	R	S	*
Sherpa	128,396	1·6	S	R	S	S
Eureka II	110,102	1·4	S	R	S	*
Charter	107,200	1·3	S	R	S	*
Sabre	93,111	1·1	S	R	S	*
Bencubbin 48	88,418	1·1	S	R	S	*
Javelin	79,538	0·9	S	R	S	S
Scimitar	75,887	0·9	S	R	S	S
Ford	65,887	0·8	S	R	S	S
Celebration	64,709	0·8	S	R	S	*
Spica	56,408	0·7	S	R	†	R
Bordan	50,042	0·6	S	R	S	S

* Reacts differentially, see Figure 5. † Reacts differentially, see Table 2.

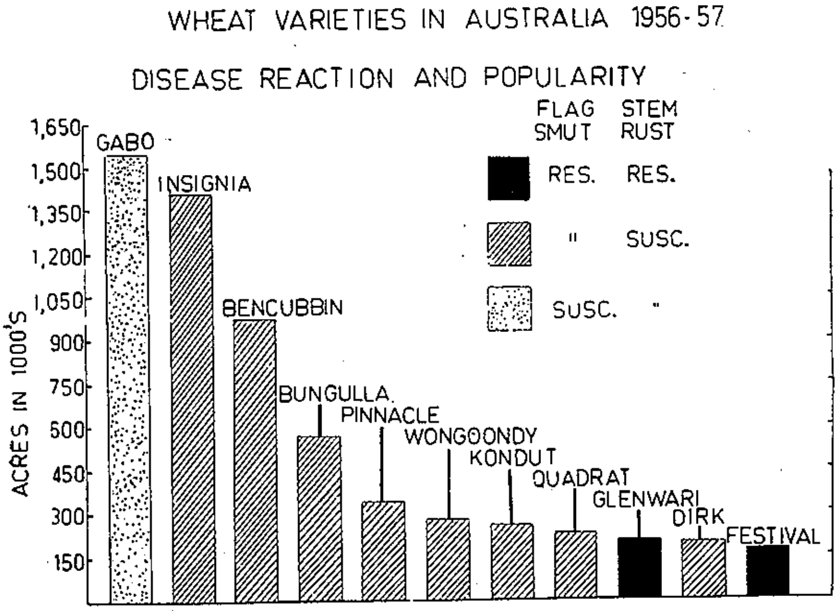

Fig. 1.—Reaction of leading Australian wheat varieties to flag smut and stem rust.

inconvenient procedure, however, and the discovery of dry dusting methods by Darnell Smith in 1915 was a distinct advance. The control was so complete there was no necessity for any extensive breeding programme and in the last thirty to forty years this disease has not damaged wheat crops where dusting operations have been performed prior to sowing. In view of this wheat breeders have tended to concentrate the attack on those diseases not readily controlled by fungicides.

During the last twenty years the most comprehensive and successful work done with bunt in Australia has been undertaken by Pugsley at Adelaide, South Australia, and more recently at Wagga, New South Wales. Such work was designed to incorporate resistance into selected South Australian varieties of wheat by back crossing.

Considerable effort has gone into the breeding of disease resistant wheats, but only in the case of flag smut has the undertaking been a complete success. It can be expected, however, that from more intensified work on the rust diseases, and through a better knowledge of the problem, more progress will be made in the future.

BUNT

A study was made of the variability of the organisms *Tilletia caries* and *T. foetida,* which are responsible for the disease in Australia. In a limited survey, Pugsley (1945) found that five races of the bunt organisms occurred throughout the wheat belt. Two were of *T. caries* and three of *T. foetida.* These were designated T_2, T_5, L_1, L_8 and L_{14}. Australian commercial varieties, with the exception of Florence and those related to it, were uniformly susceptible. None of the local varieties examined showed a resistance superior to that of Florence. However, he found that several overseas varieties (Oro, Orfed and Doubbi) are resistant to all Australian races of both species of *Tilletia.* (Personal communication from Dr. Pugsley.)

The resistance of the tetraploid variety Doubbi has been transferred successfully to a *Triticum vulgare* derivative as a result of a cross and a backcross to Ranee. The resulting resistant line has been called R.D.R. 6189. Three South Australian varieties (Insignia 49, Javelin 48 and Ridley 48) which are susceptible to all five races of bunt, were used as recurrent parents, and by backcrossing they have each been reconstituted as bunt resistant varieties. Although the Doubbi parent has maintained its resistance throughout, the recovered lines of the three above varieties have shown some variation to bunt even though the gross reaction would remain within the resistant class.

The reconstituted Ridley has been the most resistant, and the derivatives from Insignia 49 and Javelin 48 have shown some infection. Pugsley believes (1953) that these differences among resistant varieties are due partly to the race of bunt used, partly to the genotype of the reconstituted line and partly to the environment prevailing when the test for resistance was made. From studies with rust diseases, it is usual to find that the *T. vulgare* derivatives from resistant tetraploid parents seldom have the full complement of genes from the donor parent and this results in a slightly less effective resistance.

Despite the small amount of difference shown among the recovered lines the gene from Doubbi, tentatively designated "d" by Pugsley, has been successfully incorporated into bread wheat. Preliminary tests indicate that the yielding ability of the recovered lines will be equal to that of the original recurrent parent. In addition, they should possess most of the agronomic characters of the respective parents and as such, be valuable commercial varieties.

The resistance of Orfed, a variety of *T. vulgare,* has also been utilised in the production of a commercial bunt resistant variety. Yande has been developed at the Waite Research Institute by Pugsley, who used Dirk and Dirk 48 as the recurrent parents in a backcross programme with Orfed as the donor parent. Yande is not yet widely grown in any state.

Although the breeding of bunt resistant varieties in Australia is a complex problem in view of the variability of the organism, the situation in the United States is much more involved. In the Pacific north-western states bunt continues to be a serious disease, and in the five-year period 1950-1954 the annual loss in this area alone was in excess of £2,000,000. Much of the damage is caused by the well known species *T. caries* and *T. foetida.* These exist in crops extending over vast areas, and from infected plants "spore showers" are a common occurrence during the harvest period. Soil-borne inoculum becomes so concentrated that it is difficult if not impossible to control the disease by chemicals. The presence of the dwarf bunt fungus *T. contraversa* has added to the complexity of the problem. Fortunately this species has not yet been found in Australia.

Experiences in the United States can probably be used as a guide to assess the value of more intensified work in Australia, aimed at the control of bunt by breeding resistant varieties. Completely satisfactory control is obtained at present by the use of mercurial dusts, and, from a questionnaire sent to cereal workers in the various states of Australia, it is apparent that a great deal of the seed is dusted prior to sowing. This practice, even though not followed meticulously in every year, has had the effect of reducing the abundance of inoculum and this removes the hazard of "spore showers". The volume of inoculum that is distributed from field to field at harvest time in the United States, has been responsible for the problem of soil borne inoculum (Fisher and Holton (1957)) and has thus vitiated the effectiveness of seed dusts as a method of control.

While the amount of soil borne inoculum can be held in check, seed treatment should continue to give adequate control of bunt. Should the situation ever arise where seed dusting is neglected and inoculum builds up in the soil, dusts will be no more effective than they are against the soil-borne inoculum of flag smut. We would then be compelled to resort to the breeding of bunt-resistant varieties.

The prospect of having to undertake such a programme is not encouraging since the pathogenic races of the organism have played such a dominant role in the fate of resistant varieties released by plant breeders. In no other species of smut have the races become so important. Fisher and Holton (1957) show, for example, that Ridit, while remaining smut free for several years, eventually became susceptible, and others, such as Albit and Elmar, have gone the same way.

When the genes for pathogenicity are present in the smut population, segregation and recombination at each germination of a teliospore, followed by sporidial fusions, give these genes the opportunity to come together in combinations that have the ability to be pathogenic on particular combinations of genes in the host plant. The specificity that exists between races of the bunt organisms and the wheat varieties having certain genes for resistance probably accounts for the failure of a breeding programme to give a lasting protection against the disease.

While such specificity exists and while resistant varieties released for cultivation continue to have few genes offering protection, new races can readily become established once the appropriate combination of genes for pathogenicity has been assembled.

Mutation for pathogenicity in the haploid stage could also be a factor in the occurrence of new races, but no such case has been demonstrated experimentally. Mutations in other organisms are known to occur, but they probably do not come into evidence until the environment favours them.

There is no clear evidence what has taken place in the organism causing late blight of potatoes (*Phytophthora infestans*), but the specificity between the race of this fungus and the host plant genotype is so marked that potato breeders are inclined to abandon attempts to breed blight resistant potatoes by the use of major genes for hypersensitivity alone. According to Black (1957) the resistance afforded by the simple genetic system of the R genes is unreliable against blight epidemics and will eventually break down.

The situation in regard to bunt is hardly more encouraging, for as Fisher and Holton say: "Unquestionably, up to now the adaptive capacity of the bunt fungi has been equal to the best efforts of the plant scientists to control this disease through the development and release for production of resistant varieties." While this prospect faces the wheat breeders of Australia, it would seem desirable to continue with a sound policy of seed dusting for the control of bunt.

FLAG SMUT

Although Farrer makes no mention of breeding for resistance to flag smut (*Urocystis agropyri*), several of his varieties, including Florence, Bunyip, Comeback and Rymer, have been extremely valuable as sources of resistance for further breeding work in Australia. They have been used so effectively that almost all leading varieties are resistant to this disease in Australia. Gabo is the only variety that is smut susceptible and yet widely grown.

In the evolution of flag smut resistant varieties, there have been two main stems along which the varieties have evolved. According to Wenholz (1934) the Fife wheats provided the initial resistance available to Farrer. He used them very widely in crosses and this probably accounts for his success in breeding flag smut resistant wheats when he made no selections for the purpose.

Of the four varieties mentioned above, Florence, Comeback and Rymer have entered into the pedigree of Eureka, Ford and Dundee respectively. Bunyip was a parent of Nabawa and this resistance can be traced through a large group of leading modern varieties including Bencubbin, Bungulla, Wongoondy, Kondut, Javelin and Glenwari. The production of Nabawa in 1915 in Western Australia was a tremendous advance in the control of flag smut.

There is some doubt about the origin of the initial resistance used in the second main stem of the evolutionary pattern. According to the records (Anonymous 1952), the variety Currawa has contributed to the resistance shown by the Victorian wheat Ghurka, which in turn has entered into the pedigree of the varieties Insignia, Pindar, Pinnacle, Quadrat and Sherpa. Currawa resulted from the cross (Northern Champion x Cretan) x Little Club, and, since no flag smut has been found on *T. durum* in Australia to the writer's knowledge, it would seem that the resistance of Currawa has been inherited from a variety of *T. durum*.

The mode of inheritance of resistance to flag smut has not been worked out in detail, but it would appear from McMillan's work (1935) that resistance is controlled by a complex genetic system. McMillan found that, in crossing certain resistant varieties, he was able to obtain in the F_3 generation, lines that were much more susceptible to smut than the parents. This would suggest that several factors are involved and the resistance may be a polygenic character.

Breeding for resistance to flag smut has been an unqualified success and the resistance of Nabawa has been maintained for over 40 years. In view of the results obtained in similar programmes with other smut diseases, it is not easily understood. Baker and Watson (unpublished) in an extensive study of collections of smut made in all states of the Commonwealth over a period of three years, could not demonstrate consistent differences between collections on some twenty-five selected varieties.

Smut appeared from time to time on plants of resistant varieties such as Nabawa, Dundee and Ghurka, but when the variety was reinoculated with the smut taken from it no further increase in infection resulted. They concluded that slight variations found in the organism were insufficient to regard different collections as physiologic races.

The restricted variability in the flag smut organism and the complex genetical system controlling the resistance, are probably both important factors in the stability of the resistant varieties that have been bred. As long as this situation obtains the control of the disease by breeding will be a relatively simple process.

LEAF RUST

Studies already reported by Waterhouse (1952) have shown that leaf rust occurs in all wheat producing areas of Australia, but it is known that the disease is most prevalent in northern New South Wales and southern Queensland. Breeding was undertaken by Waterhouse to get resistance to the two strains that were known to occur naturally in Australia; viz., races 26 and 95. These two had been present since the early years of the commencement of rust investigations at the University of Sydney.

As a result of these investigations on leaf rust, Gabo resulted from the cross Bobin[2] x Gaza. At the time of its release, Gabo was outstanding for its resistance to leaf rust in the field to the two abovementioned races although its seedling resi tance to each was not equal to that of Gaza, the resistant *Triticum durum* parent. Small commercial sowings of Gabo were first made in the northern part of New South Wales in 1940, but it was not until October, 1945, that leaf rust was found on adult plants of this variety in the field (Waterhouse 1952).

Since 1945, Gabo has been susceptible to leaf rust throughout the eastern wheat belt, and Waterhouse concluded that four races of the leaf rust organism were present capable of attacking Gaza. One or more of them was responsible for the widespread occurrence of rust on Gabo since the latter is susceptible to all four. By 1952 six races of leaf could be readily isolated from the eastern states and they were differentiated as follows:—

Race	Webster	Thew	Gaza
26	R	S	R
95	R	R	R
135AB ...	X	R	S
135BB ...	X	S	S
138AB ...	S	R	S
138BB ...	S	S	S

R=Resistant S=Susceptible X=Mesothetic

Variability Investigations

For many years annual surveys have been made of the incidence of leaf rust throughout Australia and identifications have been made wherever possible since 1952. No collections have been received from Western Australia, but those from the eastern part of the country have been abundant. The results of this work (Watson and Luig, unpublished) will be made available elsewhere, but the following represents the reactions of the strains * of rust that have been identified.

These sixteen strains do not occur with the same frequency throughout Australia and some, such as 64-1 and 163-1, are known only in association with wheat breeders' nurseries. In general, the strains attacking Spica are found more frequently from the northern wheat zones where this variety is cultivated. Of the varieties listed in Table 1, Gabo, Festival, Glenwari and Spica are shown to react differentially to these strains. Gabo behaves like its parent Gaza, Festival as Thew, and Glenwari as Spica.

TABLE 2.

Reaction of Thew, Gaza and Spica to various strains of leaf rust organism collected throughout Australia since 1952.

Strain	Thew	Gaza	Spica
15 Anz 1 ...	R	R	R
" 2 ...	S	R	R
26 " 1 ...	S	R	R
" 2 ...	S	R	S
64 " 1 ...	S	S	R
68 " 1 ...	R	S	R
" 2 ...	R	S	S
" 3 ...	S	S	S
95 " 1 ...	R	R	R
" 2 ...	R	R	S
135 " 1 ...	R	S	R
" 2 ...	S	S	R
" 3 ...	R	S	S
" 4 ...	S	S	S
163 " 1 ...	R	S	R

R=Resistant
S=Susceptible

Sources of Resistance

The marked susceptibility of Gabo to the strains of leaf rust that developed after 1945, necessitated a concentrated hybridisation programme aimed at transferring leaf rust resistance from one or more of the common sources to a reconstituted Gabo by backcrossing.

In 1946, the following varieties were resistant: Hofed 1200† from Hope, Mentana 1124, Uruguay 1064, Timvera 1308 and Chinese White 1597. Crosses were made in that year and the resistance from Hofed was recovered in material backcrossed three times to Gabo. However, by 1951 (Watson and Singh (1952)) Hofed, Hope, H44-24 and the derivatives from them were found to be susceptible to leaf rust and no further backcrosses were made. Strain 68-4 was found on the backcross material, but 26-2 and 95-2 were also found on Hope and H-44-24.

Since these programmes commenced, Mentana, Uruguay, Chinese White and Timvera have maintained their excellent resistance as adult plants to all the strains present. Timvera has also been resistant in the seedling stage.

The resistance from Uruguay 1064 was used extensively and lines closely resembling Gabo were rapidly developed by repeated backcrossing and selection for the physiologic resistance of the donor parent. This was effective against all Australian strains of the organism known to occur at that time. After the third backcross, it became evident that when seedlings showing this type of resistance in the seedling stage to strains such as 135-4, were transplanted to the field, the reaction of the adult plant was only partially correlated with that of the seedling.

* Strain is the term that is being used to describe any collection of rust which appears to be homogeneous and which on a selected group of varieties can be differentiated pathogenically from other apparently homogeneous collections. In designating the strain number, use is made of the internationally recognised group of differential varieties as well as those essential for local determinations. The reactions on the first group are indicated by the first number. Hence strain 135 ANZ 1 gives the reactions of race 135 on the standard set of varieties and on the supplemental varieties used for this geographical area, it gives the reactions indicated. The use of the letters ANZ has been explained previously (Watson 1955). Different strains all have the same taxonomic status provided they can be readily described.

† Varieties carry the University of Sydney Accession Number.

Some resistant seedlings were resistant as adult plants, others were susceptible under field conditions where the inoculum comprised the strain that had been used on the seedlings, in addition to any that may have occurred voluntarily in the breeding nursery. Moreover, some plants which had no physiologic resistance as seedlings, were completely immune as adult plants under the same field conditions.

Investigations of the adult plants with the unexpected susceptibility in the field revealed that the anomalies were due to a difference in the strain of the organism. If seedlings resistant to a particular strain were inoculated as adult plants with the same strain, the physiologic resistance persisted throughout the life of the plant. Where resistant seedlings became susceptible as adult plants, a strain of rust hitherto unrecorded in Australia was involved. It was suspected that in those cases where susceptible seedlings became resistant as adult plants, a different genetic factor was segregating in the host and this controlled a different type of resistance.

Genetic investigations were made on this material by Athwal and Watson (1957b). These studies indicated that the mode of inheritance of resistance to leaf rust in Uruguay 1064 was relatively simple. The genotype of the resistant parent could quite adequately explain the results that had been obtained in the backcrossing programme. Uruguay was found to have two independent dominant factors concerned in resistance. One of these controlled a physiologic type of resistance which was effective against all prevalent strains such as 135-4. When this and similar strains were used in breeding it was found that the seedling and adult plant reactions were completely correlated. The same gene operated against all the strains to which Uruguay had this type of resistance.

The strain that caused the anomalous adult plant reaction of resistant seedlings, was 64 Anz 1 and it had the ability to render ineffective the factor for physiologic resistance present in Uruguay 1064. The result was that plants, selected as having this gene alone, were resistant throughout life to all local strains of the organism except 64-1 and to this they were susceptible.

Seedlings of Uruguay were susceptible to 64-1 but adult plants showed the same immunity to this as they showed to all other strains. Crosses revealed that this variety possessed an additional factor which was inoperative in the seedling stage against any local strain, but which conferred on adult plants having it, an immunity to all local strains. Selection for resistance under field conditions alone would have resulted in the transfer of this gene for adult plant resistance in the majority of the progeny. On the other hand, selection in the seedling stage would have resulted in plants largely without the adult plant factor, but possessing the factor for physiologic resistance.

The variety Chinese White, Chinese Spring and other wheats of Chinese origin are known to react with an adult plant type of reaction. When Chinese Spring 1806 was crossed with Uruguay and the progeny was studied, it was found that the gene from Chinese was present in Uruguay so that it is possible to propose the genotype of the Uruguay parent, the Gabo parent and the two types of lines recovered from backcrossing (Athwal and Watson (1957b)).

TABLE 3. Genotype of two parents and two derived lines from the cross Gabo[6] x Uruguay

Genotype					Reaction to Strain 135 — 4: As Seedling	135 — 4: As Adult Plant	64 — 1: As Seedling	64 — 1: As Adult Plant
Uruguay	Ug1	Ug1	Cw1	Cw1	R	R	S	R
Gabo	ug1	ug1	cw1	cw1	S	S	S	S
Backcross line I	Ug1	Ug1	cw1	cw1	R	R	S	S
Backcross line II	ug1	ug1	Cw1	Cw1	S	S	S	R

R = Resistant S = Susceptible

From the knowledge gained in the genetical studies it has been possible to conduct two parallel programmes of backcrossing using Gabo and certain other selected varieties as recurrent parents. One of these, carried out in the glasshouse using strain 135-4, has resulted in the transference of Ug_1 to a reconstituted Gabo after 5 backcrosses. The second line has been derived in the field where strain 64-1 has been used to select for Cw_1 in the same type of backcross material. The two homozygous lines, Ug_1 Ug_1 with physiologic resistance to all local strains except 64-1 and Cw_1 Cw_1 with adult plant resistance to all strains in this area, have now been crossed so that the factors for rust resistance in Uruguay are present in a genotype closely resembling that of Gabo. The following steps were carried out in this programme:

Step 1. Kendee was crossed with Uruguay.

Step 2. The F_1 was crossed with Gabo.

Step 3. *a.* Selections for the gene Ug_1 were made in the glasshouse using strain 135—4. Resistant plants were crossed with Gabo.

3. *b.* The hybrid plants were grown in the field and exposed to an epidemic of strain 64—1. Resistant plants were crossed with Gabo.

Steps 4. *a.* — 7. *a.* Backcrosses were repeated and $Gabo^6$ plus Ug_1 ug_1 cw_1 cw_1 plants were derived.

4. *b.* — 7. *b.* Backcrosses were repeated and $Gabo^6$ plus ug_1 ug_1 Cw_1 cw_1 plants were derived.

Step 8. $Gabo^6$ + Ug_1 ug_1 cw_1 cw_1 plants were crossed with $Gabo^6$ + ug_1 ug_1 Cw_1 cw_1 plants.

Step 9. The F_1 plants from the cross were tested with strain 135—4 in the glasshouse and the resistant ones were transplanted to the field and exposed to an epidemic of strain 64—1. Those resistant at both stages of growth were selected.

Step 10. The F_2 progeny of these plants were similarly treated and those resistant were selected.

Step 11. Homozygous F_3 lines of the genotype Ug_1 Ug_1 Cw_1 Cw_1 were obtained by testing seedlings in the glasshouse with strain 135—4 and remnant seed with 64—1 in the adult stage in the field.

It will be noted that the initial cross was Kendee x Uruguay. Since the phenotype of Gabo for factors concerned in grass clump production is AbIG and that of Uruguay is aBig, it is impossible to obtain seed from F_1 plants. Kendee, whose corresponding phenotype is bIg, is used to introduce an inhibitor which allows the Uruguay genes for leaf rust resistance to be introduced to a Gabo background. Such a backcross line with a combination of genes for resistance is now available as a useful parent in further crossing programmes.

Among the other varieties resistant to leaf rust, Mentana 1124 has been outstanding. Work by Athwal and Watson (1957a) has shown that to the common Australian strains Mentana has two linked factors for resistance. These factors usually behave as recessives in the seedling stage so that the F_1 is susceptible. One of the two genes shows a reversal to dominance, hence to the same strains of the organism, the adult F_1 plants are resistant. Mentana shows physiologic resistance to all Australian strains except 15-1, 15-2 and 163-1. To these three strains it shows adult plant resistance.

The genes responsible for the resistance of Mentana have been used extensively in breeding work and lines are now available with seven backcrosses to Gabo and Koda as recurrent parents. Previous work by Athwal and Watson (1957b) suggested that it would be possible to combine the physiologic resistance of Mentana with that of Uruguay. This has now been done experimentally and a line has been selected with physiologic resistance to all Australian strains. Ug_1 from Uruguay operates against all except 64-1 and the Mentana genes are effective giving resistance to it.

Detection of New Strains of Leaf Rust

The occurrence of new strains of leaf rust from time to time in wheat producing countries of the world, has presented a problem which has had no easy solution. In North America the incidence of new strains of *Puccinia graminis* var. *tritici* E. and H. has in many cases been correlated with barberry infections and there has been a ready explanation for sudden changes.

In Australia, much of the variability that has been shown in the organisms since breeding programmes became established, has been attributed to mutation, since the new strains have resembled the old in so many characters.

That there is good evidence for so regarding them has been gained from recent work (Watson 1957a) where it was shown that changes in pathogenicity for one variety can be readily observed in the glasshouse under controlled conditions, provided large quantities of inoculum are effectively screened. No similar work with leaf rust has been reported, but changes in pathogenicity involving one or more varieties, have been attributed to mutation since there was no other obvious alternative explanation.

For many years it has been assumed that dicaryons of the rust mycelium may undergo some type of heterocaryosis which would result in the production of new strains. In experiments at Winnipeg, Brown and Johnson (1949), failed to recover any new strains from mixtures between existing strains on wheat seedlings. Work at St. Paul, Minnesota (Watson 1957b)) demonstrated that in *Puccinia graminis* var. *tritici* some form of hybridisation took place readily between certain dicoryons, provided the parental cultures and the screening varieties were selected in such a way as to give maximum opportunity for new strains to be detected.

This work was followed by that of Vakili and Caldwell (1957), for the wheat leaf rust organism and they demonstrated a great range in the virulence of the progeny resulting from mixing two parental strains on wheat seedlings. This obviously demonstrates a mechanism for changes in virulence, which can be used to explain the origin of many new strains of this organism. It does not eliminate mutations, for these must always be a fruitful source of new genes for virulence.

Whatever the mechanism for the origin of new strains, mutation, sexual or somatic hybridisation (Watson and Luig (1958b), it is apparent that plant breeders in their hybridisation programmes facilitate the detection and isolation of new strains. Suppose, for example, there are two parental varieties, A, a susceptible one with no genes for resistance, and B, a resistant variety with four genes for resistance. Each gene gives resistance to a group of strains such that the combination will withstand the attacks of all. Before these two varieties are used in a backcrossing programme it may be considered that only one strain is present, to which A is susceptible and B resistant. When backcrossing proceeds it is unlikely that all four genes will be transferred to all progeny. Plants will occur with varying numbers of genes for resistance, from 0 to 4. New genotypes will be present sufficient to differentiate between sixteen strains of the organism. All of the strains could have been present at the commencement of breeding operations but there was no suitable genotype on which they could grow.

Two examples of such an event have occurred in the breeding for rust resistance in New South Wales. They serve to demonstrate the importance of splitting gene combinations in relation to the detection of new, pathogenic strains of wheat leaf rust.

The first example has been mentioned already in connection with the isolation of strain 64-1 from the Gabo x Uruguay backcross material. It will be seen from Table 3 that the parental combination of genes has remained effective against all strains, whereas the Ug_1 Ug_1 cw_1 cw_1 component, split off from the original, became specific for the isolation of strains that render ineffective this particular gene Ug_1. We have since shown that Norka and Malakoff apparently carry the gene specific for 64-1 from Uruguay. Although these latter varieties have been grown regularly in the nursery and have been used in all routine testing they had always proved resistant until the appearance of 64-1.

The second example comes from the backcrossing programme with Mentana. Field observations for several years and genetic studies by Athwal and Watson (1957a), had shown that the resistance of Mentana in the adult plant stage was dominant to susceptibility, irrespective of what variety was used in the cross as the susceptible parent. Reaction of adult plants had been the basis of the procedure in successfully transferring the resistance of Mentana to several recurrent parents. After the fifth backcross to Gabo of a Gabo x Mentana cross, all F_1 plants were susceptible. Isolations were made from the rust present and it proved to be a strain new to Australia, 163-1. It is characterised by its virulence on Mentana (seedlings only), Webster and Gaza.

The detection of the rust on the F_1 plants of Gabo ^{6} x Mentana is considered to be associated with the removal of the effects of one of the genes of Mentana due to lack of dominance of this particular gene. Instead of two genes for resistance, the F_1 has only one operating and is thus more exposed to mutation and new combinations of virulence genes, possibly resulting from somatic hybridisation. This can best be illustrated by reference to Table 4.

TABLE 4. Reaction of Gabo, Mentana and their F_1 to two strains of *Puccinia triticina*.

Genotypes		Reaction to Strain 135—4 As Seedlings	135—4 As Adult Plants	163—1 As Seedlings	163—1 As Adult Plants
Gabo	$mt_1\, mt_1\, Mt_1\, Mt_2$	S	S	S	S
Mentana	$Mt_1\, Mt_1\, mt_2\, mt_2$	R	R	S	R
F_1	$Mt_1\, mt_1\, Mt_2\, mt_2$	S	R	S	S

R = Resistant S = Susceptible

According to previous studies the two genes of Mentana can be listed as Mt_1 and mt_2. Both operate throughout life to strains such as 135-4. As seedlings both are recessive, Mt_1 becomes a dominant in the adult plant stage. This means, on the gene for gene theory, that a mutation at two loci simultaneously would be necessary for Mentana to become susceptible. In a somatic hybrid it means that two virulence genes must come together in the same strain.

When the F_1 is exposed in the field to an epidemic, only one source of resistance is operating, namely Mt_1 since mt_2 is recessive to Mt_2. A mutation in the rust at the locus controlling the reaction of Mt_1 such that it becomes ineffective, would mean that the genotype $Mt_1\, mt_1\, Mt_2\, mt_2$ is susceptible both in the seedling and the adult plant stage. While this appears the most likely explanation, irrespective of whether the strain has arisen as a mutation or as a somatic hybrid, inheritance tests using 163-1 have not yet been completed to verify certain assumptions.

The results obtained from the two above methods of splitting a combination of two genes, show that a plant breeder's nursery is a very fruitful source of new pathogenic strains. However they also have considerable significance from the point of view of breeding for rust resistance. They suggest that the effects of backcrossing and the utilisation of multiline varieties as proposed by Borlaug (1957), will facilitate the detection and isolation of a multiplicity of strains which are specific for the genes of the hosts that have been fixed during backcrossing and selection. It is conceivable that many of these will represent virulence genes that hitherto have not had access to a genotype on which they can survive in a population. Whether such genes become economically important in causing damage to the components of the multiline variety, will be governed by a number of factors.

The fact that Uruguay and Mentana have themselves remained resistant to leaf rust while progeny carrying only portion of their genotype have become susceptible to new strains, suggests that combined resistances as a method of breeding has considerable merit. It is most likely that genes for virulence in the organism occur with widely different frequencies in the population, so that the chances of a particular gene of the host becoming ineffective through recombination in the pathogen, will differ from gene to gene. The fact that in each variety the gene for hypersensitivity in the seedling stage became ineffective may be more than a coincidence. Results obtained by Athwal and Watson (1957a), indicate that the genes in Mentana are unrelated to those in Chinese Spring so that there are, in Mentana and Uruguay, two sources of adult plant resistance both of which have withstood the changes that have taken place in the organism. Possibly the Chinese type of resistance, which so far has operated regardless of strain, will be the most valuable for a lasting resistance.

Physiologic resistance to all of the Australian strains of leaf rust are rare and since no single gene has been known in the past which could give a comprehensive resistance to all, the two types of resistance from Mentana and Uruguay have been combined. Only one other such resistance is known which is effective against all local strains. This has been derived by Sears (1956) from *Aegilops umbellulata.* The mode of inheritance of this resistance has not yet been worked out for Australian strains of leaf rust, but evidence from preliminary studies indicates that it is simple. Steps have already been taken to combine this resistance with some of those already available, and thus still further broaden the genetic base on which resistance to leaf rust depends.

STEM RUST

The stem rust problem as viewed by Farrer at the turn of the century would probably have appeared a relatively simple one. He started his work when the fundamental knowledge of the disease was lacking, not only in Australia, but in other wheat producing countries as well. He was unaware of the extreme variability that was present in the organism and which was later to upset breeding programmes in many countries.

There is little information available to show which of the strains of rust were present throughout the country when Farrer worked, but the classification of varieties given by Waterhouse (1938) shows clearly that certain of Farrer's varieties were resistant to all of the strains that were present prior to 1925. From the records it is not clear which of these varieties were selected under epiphytotics in the field.

With the information gained from surveys of the organism, Waterhouse was able to plan a breeding programme aimed to get resistance to all the strains present. Euston, which fulfilled this requirement, arose from the cross Canberra x Thew. In 1926, a strain which was designated race 34, appeared for the first time, and Euston, as well as many other varieties, became susceptible. (Waterhouse (1952).)

About the year 1930, a greatly expanded programme of breeding for rust resistance was commenced. This coincided with the discovery of several new parents which were introduced from overseas. Webster and Hope were received from the United States and from the cross Federation x Webster, Waterhouse named Fedweb. Hofed resulted from the cross Federation x Hope. Both varieties were resistant to all strains of stem rust in 1936, and they have maintained that resistance to the present time. However, they are not well adapted to the conditions of the northern wheat belt, and although they were the first rust resistant commercial varieties available their combined acreage was not large.

The New South Wales Department of Agriculture introduced the Kenya varieties from East Africa and these played a major part in the expanded breeding programme. Almost nothing was known at the time of the genetics of resistance to wheat stem rust in Australia and it was not fully appreciated that the Kenya wheats available, Kenya 743 (C6040)*, Kenya 744 (C6041) and Kenya 745 (C6042) each contained a distinct type of resistance (Watson 1943, Watson and Waterhouse 1945).

From one of these Kenya wheats (C6040), Macindoe developed three variety Eureka from the cross Kenya x Florence x Dundee. It was agronomically attractive, was immune to all known strains of stem rust and produced a good quality grain. Consequently, it was accepted readily by growers and the area sown to it increased from 4,198 acres in 1939-40 to 48,731 acres in 1940-41 in New South Wales. At a stage when the rust problem appeared to be solved, Eureka and its Kenya parent became fully susceptible and a new strain of stem rust, hitherto unrecorded in Australia, was isolated from it. It was designated race 126B (Watson and Waterhouse 1949).

Although Kenya 743 was now of little value, the other two introductions 744 and

* The first number is the University of Sydney Accession number. The second the Accession number of the New South Wales Department of Agriculture.

745 remained resistant and the progeny of crosses that had been made with them were developed as varieties. Kenya (C6042) had also been used by Macindoe and he produced Yalta (Kenya x Pusa 4 x Dundee) and Charter (Kenya x Gular). Waterhouse produced Kendee from the cross (Dundee x Kenya 745) and all three derivatives of this Kenya variety have been successful commercial varieties.

The resistance of Gaza (*T. durum*) was also utilised by Waterhouse about the same time. Gabo resulted from the cross Bobin[2] x Gaza. Since Eureka had failed as a resistant variety, Gabo, Yalta, Charter and Kendee were rapidly multiplied to replace it in northern New South Wales. This they did satisfactorily as all were high yielding varieties of satisfactory grain quality. Studies on the nature of their resistance, however, showed that although one was a derivative of *T. durum* they all possessed the same genetic factor for resistance to the common strains. As a result of this, it was predicted that should one become susceptible to a new strain, all four would be similarly affected. (Watson and Waterhouse 1949). In view of this possibility an intensified programme of breeding, using diverse sources of resistance was commenced immediately (Watson 1949). Before this could make much headway, however, the four abovementioned varieties became susceptible to at least two new strains of stem rust (Waterhouse 1952). Since that time, Kendee and Yalta have been practically eliminated from the rust liable areas of the State, while Gabo and Charter, being somewhat less susceptible, are still grown successfully.

The third source of resistance present in the original introductions from Kenya, (744, C6041) has been the parent of three varieties, namely Festival (Pusa 111 x Kenya x Baringa), Dowerin (Sword x Kenya) and Moora (Sword x Kenya) x Eureka. The resistance present in this Kenya variety has been maintained against all Australian strains of stem rust.

In addition to the Kenya varieties, Macindoe used the resistance of a Double Cross line closely related to Thatcher. From the cross Dundee[2] x Double Cross, he named the variety Celebration. The latter maintained its resistance to all local strains of stem rust from 1942 to 1954, but in that year it became susceptible to a strain that was first isolated from several places in southern New South Wales, Victoria and Tasmania (Watson 1955). With the occurrence of a strain capable of attacking Celebration, the fourth major change in the stem rust strains since 1920 had occurred. Each change was associated with a specific type of resistance in the host, although race 34 in 1926 was able to attack several varieties previously resistant. Following the appearance of strain 21-1 in 1954, a further strain, 21-2, was isolated from Woodburn, New South Wales in 1956 (Watson & Luig 1958b). It differed from 21-1 in that Gabo was susceptible.

Varieties having the Hope type of resistance have maintained their resistance since their release. No strain capable of attacking Hope has been found in Australia during thirty years of study. Spica with the pedigree (Three Seas x Kamburico) x (Pusa x Flora) has also maintained its resistance for several years.

The Life Cycle of the Stem Rust Organism

In contrast to the situation in the northern parts of North America, the wheat stem rust organism in Australia can readily pass from season to season on the cereal host and on susceptible grasses (Waterhouse 1952).

Irregularity of the infections on barberry, the alternate host, has probably been of considerable importance in restricting the variability of the organism since the aecial infections found by Waterhouse (1934) were correlated with the occurrence of certain new strains of the organism. Since several of the new strains have been isolated for the first time, many hundreds of miles from areas where barberries are known to occur, sexual hybridisation is not the only factor in variability of the organism in Australia.

New strains which occur from time to time in barberry areas can result from crosses between existing strains, or they may be among the inbred progeny of a single strain. Strains which are weakly pathogenic because they have many dominant factors for avirulence may, if heterozygous, give rise to virulent strains among the progeny due to the accumulation of recessive genes. This has been known for many years to be the danger of barberry infection and in Figure 2 a typical result of inbreeding is shown.

In this case an original avirulent strain, to which Little Club was susceptible and Acme, Mindum and Einkorn were resistant, was selfed on barberry and aecidiospores obtained. Many virulent strains were recovered as progeny when these spores were placed on wheat seedlings and three of them are shown in this figure. One attacked Acme, the other Einkorn and the third was virulent on Mindum.

Under laboratory conditions it is possible to predict the nature of the progeny that will be recovered when barberries are infected by known strains. Under natural conditions in the field, however, the multiplicity of strains present makes this impossible and herein lies the menace of barberry in the wheat stem rust problem.

The strains that have arisen in connection with the breeding programme in New South Wales, are considered to have probably appeared as a continuing process of mutation (Waterhouse 1952). This is reasonable in view of the very close similarity between all the strains of rust that have been prevalent since 1925. Strains isolated from 1939-1952 fall mainly within the categories of race 126 or 222 and all show the temperature sensitive reactions of Arnautka, Mindum and Spelmars. They would appear to have had a common origin and are typical of the type of mutant that was isolated in the glasshouse, when large volumes of uredospores of pure cultures were screened (Watson 1957a).

Since 1954, however, a dramatic change has occurred among the prevalent strains of eastern Australia. This occurred first with the appearance of 21-1 and more recently, with 21-2. In view of their avirulence on Kanred, a character typical of these strains, it is difficult to attribute their origin to mutation.

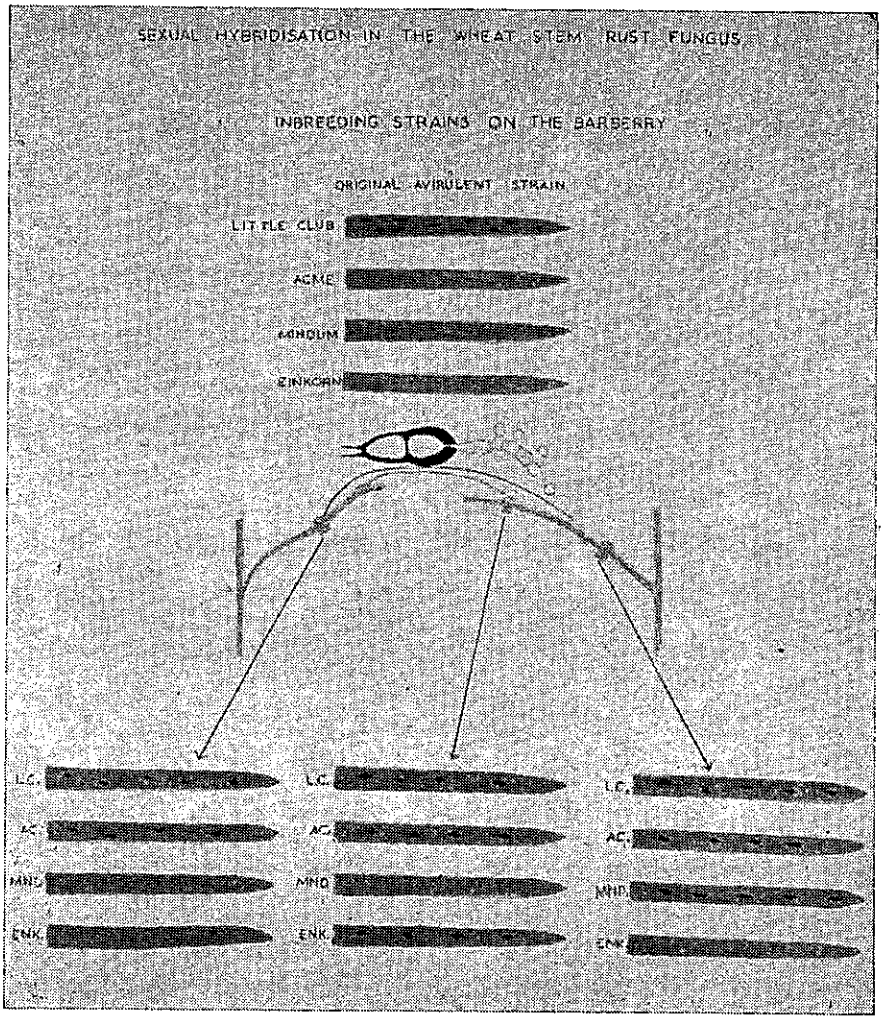

Fig. 2. — Virulent progeny obtained by inbreeding an avirulent strain of stem rust on barberry.

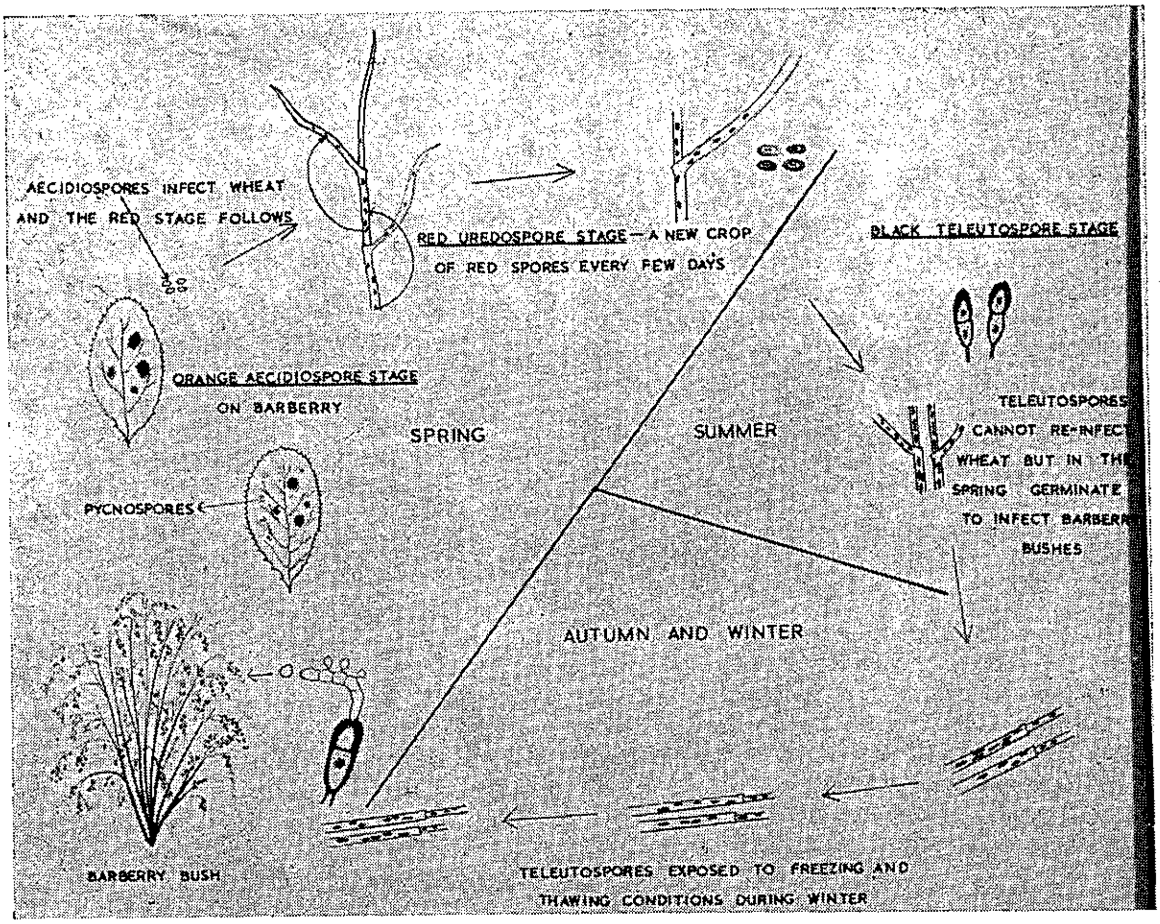

Fig. 3.—Life cycle of wheat stem rust in areas such as Tasmania where barberries are readily infected.

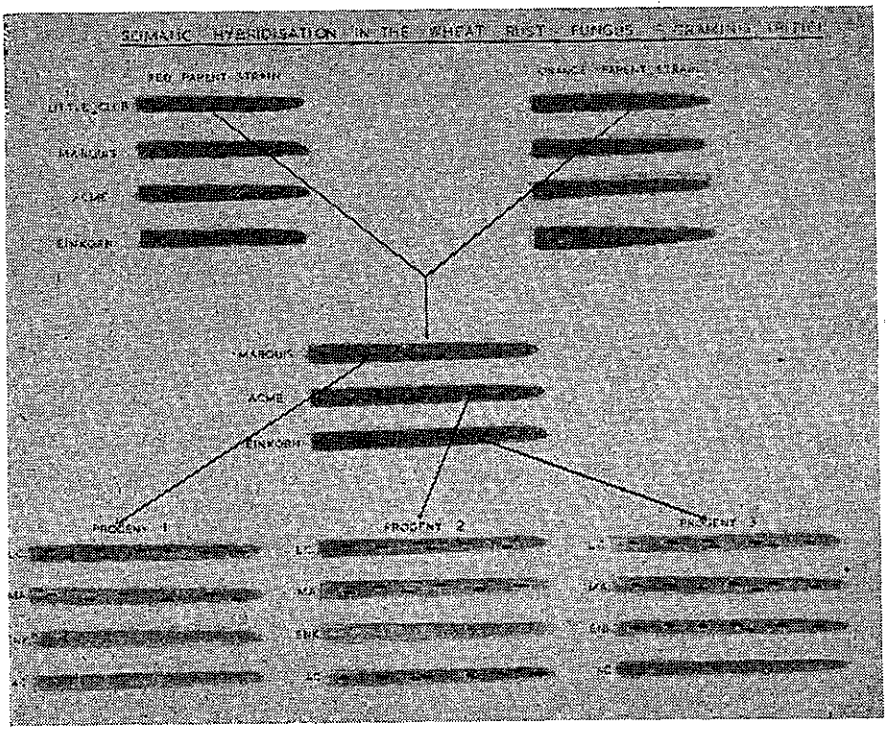

Fig. 4. — Virulent progeny recovered when a red avirulent strain was mixed on wheat seedlings with a virulent orange strain.

Barberries, which are now known to be widespread in Tasmania, have been found infected with stem rust in the last two years (Watson and Luig 1958a). It is considered that strain 21-1 had its origin in the barberry areas of that State and spores moved north to the mainland. This explanation would necessitate the dominant gene for avirulence on Kanred being present in the local rust population. While this gene has been found only rarely in collections made between 1925 and 1954, it was high in frequency among the collections made prior to 1926 (Waterhouse, 1952). Since the six common races collected in this latter period were unable to attack Kanred, this gene for avirulence was clearly of importance at one stage. A strain containing it may have been involved in barberry infections which produced 21-1.

In Figure 3 the life cycle of wheat stem rust is shown diagramatically for areas typical of Tasmania. It is now recognised that while the bulk of the inoculum survives as viable uredial material throughout Australia, certain restricted areas have an environment which provides wheat stem rust with the opportunity to complete its full sexual cycle. These areas must be watched carefully as Luig and Watson (unpublished) have already obtained virulent strains by infecting barberries with 21-1 in the glasshouse. Such strains will arise in the field once barberries are infected with the appropriate material.

Mutation and sexual hybridisation on the barberry are processes which result in new pathogenic strains. It is now known, however, that these latter can also arise both in the laboratory and the field by somatic hybridisation on wheat plants (Watson and Luig, 1958b). In the example shown in Figure 4 a red Einkorn strain, avirulent on Marquis, Acme and Einkorn was mixed on these three varieties with an orange strain to which all three were susceptible. The resulting red pustules, which were formed by the hybrids between the two parents, were taken from the leaves of Einkorn, Marquis and Acme. On these varieties and Little Club, the progeny of each pustule was established as a new strain.

The details enabling this type of hybridisation to occur have not yet been worked out, but when certain strains are mixed, hybrid progeny can be isolated without difficulty. This means that under Australian conditions, at least three processes are available by which the stem rust organism may change its virulence. Of these, barberries could be undoubtedly the most spectacular if large areas of susceptible wheat were grown in Tasmania. Since this alternate host is seldom infected in areas of commercial wheat growing, the importance of another process has been recognised.

Strains of Wheat Stem Rust in Australia

In 1952 Waterhouse summarised the reaction types and prevalence of races of rust that he had found throughout the country during over thirty years of study.

Since this time the investigations have continued and most of those races reported by Waterhouse have been recovered. Additional ones have been isolated from specific varieties in plant breeders' nurseries.

In Figure 5 the reactions of the strains which have been found since 1952 are given, together with their distribution throughout Australia. Strains 34-2 and 222-4 have only been found in association with plant breeders' nurseries in the County of Cumberland, N.S.W., and are regarded as rare types. 126-1 which is probably identical with race 34 described by Waterhouse, is widely distributed, but not prevalent in the Eastern States. It is the only strain known to occur in Western Australia.

Fluctuations in Straw Prevalence in the Northern and Southern Wheat Zones

Wheat stem rust is usually more prevalent in northern New South Wales and Queensland than in the other parts of the wheat belt.

Resistant varieties that have been produced have therefore had special application in these areas. The pattern of the varieties grown in any area will markedly affect the prevalence of strains found there if resistant varieties have a differential effect.

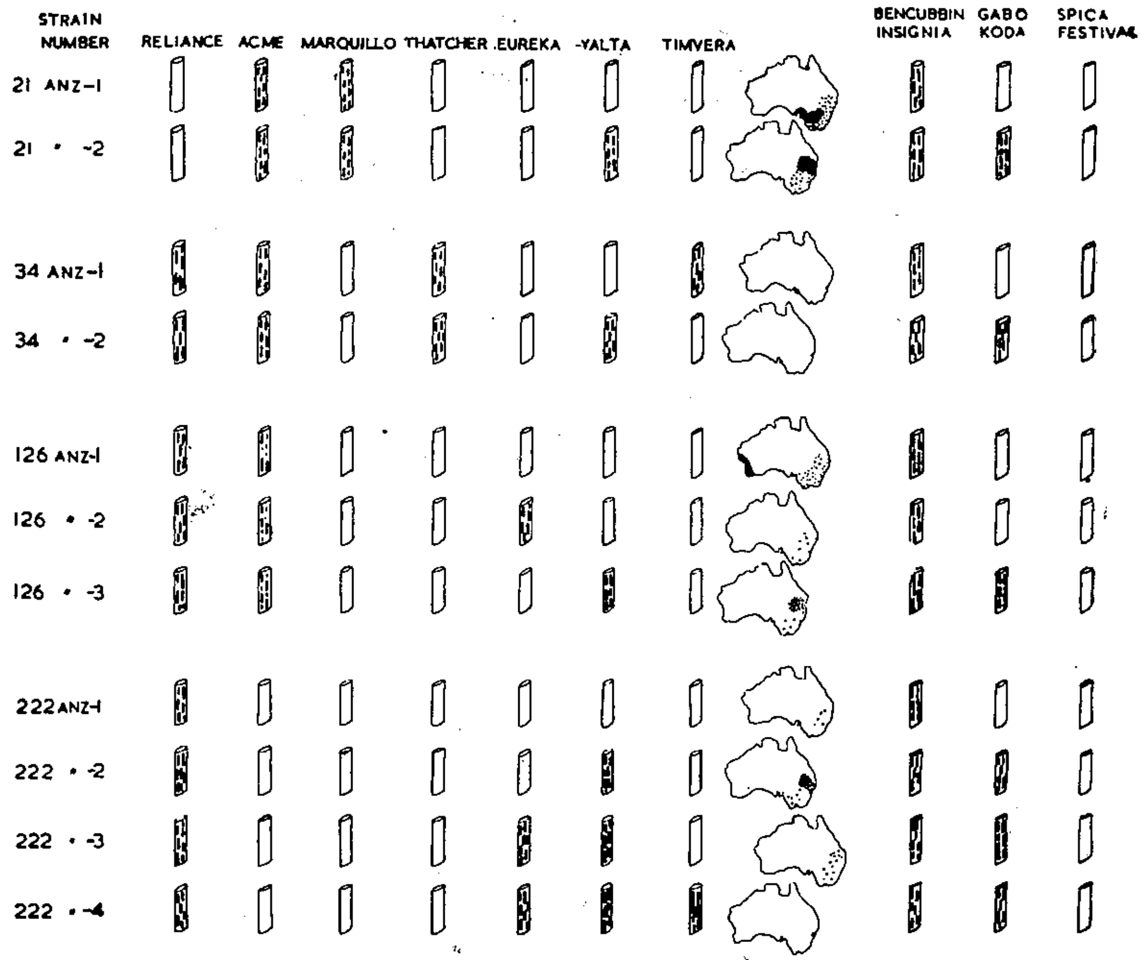

Fig. 5.—Reactions of selected regular differential, supplemental and commercial varieties to eleven strains of wheat stem rust. Blackened stems represent susceptibility and the intensity of stippling on the map is correlated with strain prevalence. Wongoondy reacts as Eureka; Kendee, Bencubbin 48, Sabre and Charter as Yalta; Celebration as Marquillo; Kanred as Reliance; W 1656 as Timvera; Glenwari and Warigo as Spica.

NOTE.—The reactions of Marquillo to strains 34 ANZ 1 and 34 ANZ 2 are those at low temperatures.

For this reason, it has been essential to separate areas where Gabo is among the leading varieties, from those where the varieties are mostly of susceptible types. The dividing line between the two zones has been taken as the Western Highway which runs from Sydney to Bathurst, Orange, Wellington, Dubbo and Trangie. Areas north of this line have been grouped with Queensland, areas south of the line have been grouped with Victoria for purposes of analysing strain prevalence.

Variations in prevalence of strains in the northern areas have been influenced firstly, by the cultivation of Eureka and more recently, by varieties such as Gabo, Charter, Yalta and Kendee which as stated above have a similar, if not identical factor for resistance. In Table 5 the acreages sown to Eureka for the year 1939-40 to 1956-57 are given. The statistics are not complete since records were not kept during the war years but the table shows that Eureka was readily accepted by farmers and it occupied 19.2 per cent. of the total area for the zone in 1945-46. It became susceptible in 1941 but its popularity did not recede immediately as there were no suitable varieties to replace it.

TABLE 5.

Acreages sown to Eureka and to varieties with the Gabo type of resistance from 1939-40 in northern New South Wales together with the percentage of each in the total area.

Year	Eureka			Gabo Type		
	Acreage	Per Cent of Area	Per Cent Frequency of Eureka Rust Strains	Acreage	Per Cent of Area	Per Cent Frequency of Gabo Rust Strains
1939–40	4,021	0·3	......	......	......	......
1940–41	44,202	3·0	......	......	......	......
1941–42	*	......	8·3	......	......	......
1942–43	*	......	25·0	......	......	......
1943–44	*	......	41·7	......	......	......
1944–45	*	......	47·6	......	......	......
1945–46	219,295	19·2	72·4	13,742	1·2	......
1946–47	141,771	7·9	63·6	115,486	6·4	......
1947–48	*	......	55·4	*	......	......
1948–49	18,034	1·3	55·2	698,775	49·8	13·8
1949–50	*	......	56·2	*	......	85·1
1950–51	17,929	1·8	64·8	633,737	62·4	90·8
1951–52	20,004	1·8	30·8	486,533	43·7	76·9
1952–53	18,691	1·5	45·8	528,450	42·6	79·2
1953–54	12,936	1·1	7·1	632,679	52·8	76·2
1954–55	9,109	0·8	18·1	612,008	45·4	53·4
1955–56	9,196	0·7	10·3	695,970	53·7	32·5
1956–57	5,641	0·7	......	500,066	58·4	64·3
1957–58	*	......	......	*	......	96·3

* = no figures available

An examination of Table 5 and Figure 6 will show the relation between the area sown to Eureka and the frequency of isolation of the strains to which it is susceptible. These latter include 126-2, 222-3 and 222-4 and they reached a peak in the year 1945-46 when the area sown to Eureka was at its highest. Since that time, there has been a steady fall in the area sown to this variety and this has resulted in a corresponding decline in the frequency of isolation of strains capable of attacking it. For the two-year period 1956-58 no strains virulent on Eureka have been found. The frequency of isolations of the rust have included samples collected in the northern zone of New South Wales and Queensland. The figures for 1941-1951 have been taken from those of Waterhouse (1952) and it is probable that there is some bias in the number of isolations of strains virulent on Eureka as many of his collections were made on this variety.

There is close correlation between the area of Eureka sown and the number of collections which comprised strains specific for it.

The rarity of such strains in 1956-58 is confirmed by observations in the wheat belt and a typical reaction in the field during recent years is shown in Figure 7. Although more than 5,000 acres of Eureka are still grown in the area, no crop has been damaged by rust in recent years. Infection has been found on Eureka from time to time, but the rust has not proved to be virulent. In all cases it has been of 21-1 or 21-2. The variety Bowie, which has a resistance similar to that of Eureka but of a somewhat higher order, has also been immune to stem rust in the northern zone.

The cultivation of varieties with the second type of resistance, viz., that of Gabo-Kenya 745, began during the war years and statistics of acreages in the early stages are therefore unavailable. The first figure shown in Table 5 is 13,742 acres of Charter for 1945-46; for all following years where areas sown were recorded, the figures include the combined acres of all varieties known to have this type of resistance. These are Gabo, Charter, Kendee, Yalta, Javelin 48, Sabre and Koda. The highest percentage of the northern zone sown to wheats of this

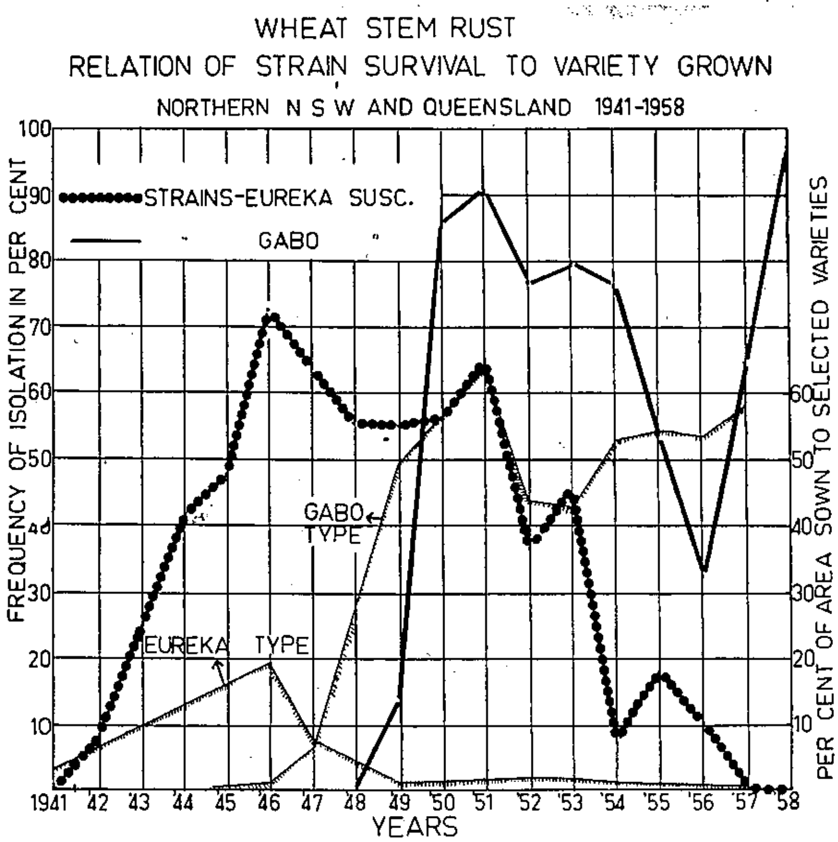

Fig. 6.—Acreage in northern New South Wales sown to Eureka and to varieties with the Gabo type of resistance together with the percentage frequency of isolation of strains from northern New South Wales and Queensland to which these two groups of varieties are susceptible.

sort was in 1950-51 when the figure was 62.4. Since that time the areas have been rather consistant and represent between 50 and 60 per cent. of the total.

The prevalence of strains corresponding with acreages of specific varieties, is again evident when the Gabo-Kenya 745 resistance is considered. Strains attacking Gabo and other varieties of the group were first isolated in 1948-49 and constituted 13.8 per cent. of the total isolates for that year from this zone. Those that are virulent on Gabo include strains 21-2, 34-2, 126-3, 222-2, 222-3 and 222-4.

The steady increase of areas sown to varieties with the Gabo-Kenya 745 resistance continued up to 1950-51 and is paralleled by the increase of the strains virulent to them, with a prevalence of 90.8 per cent. in 1951. Despite a relatively constant area of this type of variety from 1953-54 onwards, the frequency of isolation of strains attacking them failed to be correlated for the two-year period 1954-1956. Results from the rust survey as a whole reveal that this lack of correlation was due to the rapid increase in prevalence of strain 21-1 during the years 1954-55, 55-56 as shown in Table 6 and Figure 8.

This strain 21-1, which was first isolated in the southern zone rapidly spread to the northern zone and increased on crops of Bencubbin and varieties having little resistance to it. It was unable to attack wheats of the Gabo-Charter group but nevertheless it was frequently isolated from the northern zone. This widespread distribution reduced the percentage prevalence of strains virulent on Gabo and accounts for the figure 32.5 per cent. for these latter in 1956.

Table 6. Rise in Prevalence of strains 21—1 and 21—2 in Eastern Australia over a five year period.

Year	1954	1955	1956	1957	1958
Percentage Prevalence	......	14·1	71·2	82·4	85·7

Fig. 7. — Resistant reaction of Eureka (E) grown under epidemic conditions at Castle Hill in 1958. The check is Federation (F) broken down following severe rust infection. The strain causing the damage was mainly 21-2.

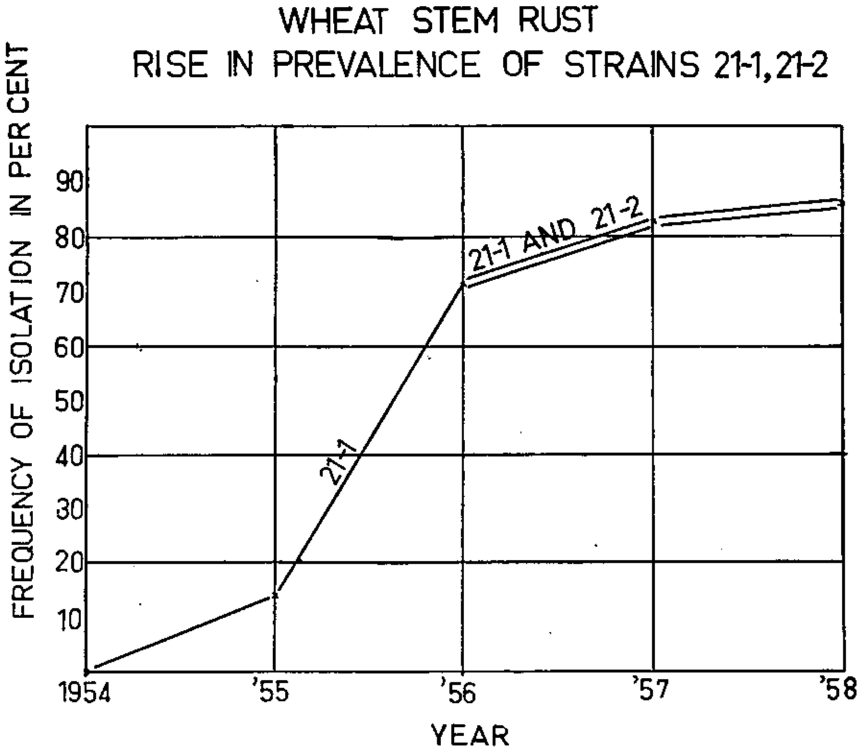

Fig. 8.—Graph showing rapid rise in prevalence of strain 21-1 from 1956 and that of both strains 21-1 and 21-2 in eastern Australia.

The widespread cultivation of wheats of the Gabo class placed a definite limitation on the spread of this strain in the north. However, the experience in eastern Australia has been, that when prevalent strains occur in areas where varieties with a hypersensitive type of resistance predominate, the organism, by some means, adapts itself so that the hypersensitivity is no longer effective in giving protection. The results on a field scale have been similar to those obtained in the glasshouse under controlled conditions (Watson 1957 a).

The adaptive process in this instance resulted in the strain 21-2 which, like 21-1, is very aggressive but in addition, has the specific ability for virulence on varieties with the Gabo-Charter type of resistance. In Figure 8 the double line in the graph represents the combined percentages of strains

21-1 and 21-2, the latter strain being especially abundant in northern New South Wales and Queensland.

Strain 21-2 is believed to have arisen from 21-1 (Watson and Luig 1958 b). It could have arisen by mutation, since only a single source of resistance differentiates it from 21-1 and thus only a single step mutation would be involved. We have been unable to distinguish it from 21-1 on any variety other than those with the Gabo-Kenya 745 resistance. Watson and Luig (1958 b) have recently demonstrated, however, that it could also have arisen as a somatic hybrid between two parental strains 21-1 and 222-2 which were both present in the northern wheat zone where 21-2 was first isolated.

These two strains together have the characters found in 21-2 and the latter was recovered as one of the progeny when strains 21-1 (orange) and 222-2 (red) were mixed on wheat seedlings. Genetical studies have not yet revealed whether the 21-2 produced in the laboratory is identical with that in the field, but the reactions of parents and progeny are given in Table 6A.

TABLE 6A.

Reactions of 3 wheat varieties to strain 21—2 and two parental strains from which it was derived by somatic hybridisation.

Parent Strain	Progeny	Uredospore Colour	Variety		
			Kanred	Gabo	Celebration
21—1	....	Orange ...	R	R	S
222—2	....	Red	S	S	R
21—2x222—2	21—2	Red	R	S	S

R = Resistance S = Susceptibility

Whatever the mode of origin, strain 21-2 has largely replaced 21-1 in the northern zone in the last two years and because of this the percentage frequency of isolation of strains virulent on Gabo has risen from 32.5 in 1956 to 96.3 in 1958. It is apparent from Figure 6 that in the northern zone, the strains of greatest prevalence are those to which Gabo is susceptible and Eureka resistant.

The influence of the varietal composition on the prevalence of strains found in the northern zone, has also been found in the southern zone. In this latter, stem rust has not developed so consistently and the areas sown with varieties having one or other of the two types of hypersensitivity, have never been large. When the areas sown to Eureka and to varieties having the Gabo-Kenya 745 resistance are considered as in Table 7 it will be seen that the percentage does not approach that in the north. The highest acreage was in 1945-46 and there has been a downward trend since that time.

After a peak of 70.3 per cent. in 1950-51 for the prevalence of strains virulent on Eureka, there has been a steady decline to 0.0 in 1958. The Gabo-attacking strains were at their maximum prevalence also in 1950-51 and they have declined to 10 per cent. of all isolates collected in the zone for 1958. In contrast to the north, the strains in the south, which consist mainly of 21-1, are avirulent both on Eureka and on Gabo.

Relation between Virulence Factors and Survival of Strains

In an extensive study of the flax rust organism *Melampsora lini*, Flor (1956) has found that the strains with the widest host range and therefore having the most factors for virulence, do not, as a rule prevail with the greatest frequency.

Flor considers that the strains with the lowest number of virulence factors necessary for survival are those that predominate. The same principle appears to hold in the wheat stem rust organism under Australian conditions. Under laboratory conditions, Watson and Singh (1952) have demonstrated that strains with a wide host range are unable to maintain themselves in a population when grown on Federation seedlings in association with strains having a narrower host range. Under conditions of equal opportunity, such as might obtain on uniformly susceptible Federation seedlings, the virulent strains apparently lack certain factors necessary for survival. Up to date it has not been possible to relate any single character of strains to their differential survival ability.

The medium of a uniformly suspectible variety is simulated to some extent in the field in those areas where the variety mixture is mainly of susceptible types. A study of strain prevalence in such areas would be a guide to the competitive and survival ability of strains. The wheat grown in southern New South Wales and Victoria approximates as closely to a uniformly susceptible type as it would be possible to find in Australia. In this southern zone the main varieties are Bencubbin, Insignia and Pinnacle. These have no genes for hypersensitivity and do not react differentially to the Australian strains. If all strains have approximately the same abilities, they should be recovered from these areas with about the same frequency. Such a situation has never been found to exist.

TABLE 7.

Acreages sown to Eureka and to varieties with the Gabo type of resistance from 1939–40 in Southern New South Wales and Victoria together with the percentage of each in the total area.

Year	Eureka Type			Gabo Type		
	Acreage	Per Cent of Total Area	Per Cent Frequency of Eureka Rust Strains	Acreage	Per Cent of Total Area	Per Cent Frequency of Gabo Rust Strains
1939–40	nil	......	......	nil	......	......
1940–41	nil	......	......	nil	......	......
1941–42	*	......	......	*	......	......
1942–43	*	......	7·1	*	......	......
1943–44	*	......	40·0	*	......	......
1944–45	*	......	50·0	*	......	......
1945–46	64,555	1·1	20·0	2,812	0·1	......
1946–47	53,873	0·9	48·6	37,282	0·6	......
1947–48	*	......	43·9	*	......	......
1948–49	60,298	1·0	53·6	280,532	4·7	......
1949–50	*	......	61·8	*	......	44·9
1950–51	33,045	0·6	70·3	341,259	6·6	59·4
1951–52	28,505	0·7	36·8	360,883	8·1	26·3
1952–53	18,551	0·5	22·2	340,844	8·7	16·7
1953–54	35,632	0·7	10·0	352,068	7·4	25·0
1954–55	27,234	0·6	16·6	274,097	6·1	38·0
1955–56	27,421	0·7	3·7	296,242	7·4	13·3
1956–57	17,200	0·7	......	174,957	6·9	16·1
1957–58	*	......	......	*	......	10·0

* = no figures available

When the effect of variety is removed, certain strains predominate, due presumably to a combination of characters which endow them with the ability to compete with associated strains and eventually to overrun them in the population. Such a happening occurred after race 34 (126-1) was first isolated from eastern Australia in 1926 and it has been repeated with strain 21-1 since 1954.

Strains of stem rust recorded in eastern Australia can be divided conveniently according to their reaction on varieties having one or other of the two hypersensitive resistances mentioned above. If this is done the following classification results:—

Group 1. Eureka resistant, Gabo resistant —strains 21-1, 34-1, 126-1, 222-1.

Group 2. Eureka susceptible, Gabo resistant—strain 126-2.

Group 3. Eureka resistant, Gabo susceptible—strains 21-2, 34-2, 126-3, 222-2.

Group 4. Eureka susceptible, Gabo susceptible—strains 222-3, 222-4.

The frequency of each of these four groups of strains found since 1952 in the southern and the northern zone of the wheat belt is given in Table 8.

It is apparent from Table 8 and Figure 9 that the avirulent strains predominate in those areas of the country where the main varieties grown are susceptible. Ninety-one per cent. of the isolates in 1958 were of such strains. The more virulent strains specific for their ability to attack either Eureka or Gabo only become of major importance in the area where the growing of these varieties necessitates this ability.

TABLE 8.

Frequency of isolation in Per Cent of strains classified according to their reaction on Eureka and Gabo

Year	Southern Zone Group				Northern Zone Group			
	1	2	3	4	1	2	3	4
1952	36	18	36	9	15	8	54	23
1953	66	17	11	6	0	17	52	30
1954	70	5	20	5	23	2	71	5
1955	59	3	24	14	43	3	39	15
1956	84	2	13	0·4	67	1	23	10
1957	83	0	17	0	36	0	64	0
1958	91	0	9	0	3	0	97	0

Strains such as 222-3 and 222-4 which have a combination of two special abilities at least, are the lowest in frequency. In the northern zone, where the Gabo-Kenya 745 type of resistance exists in the leading varieties, a special ability is required in the fungus to enable it to survive and become a major component of the population. The avirulent strains are thus confined to occasional areas of congenial hosts and their frequency is correspondingly reduced. Strains such as 126-3, 222-2 and more recently 21-2 have therefore tended to prevail in this zone.

A closer examination of the frequency of the strains recovered from the north and from the south make it clear that the predominant strains have the minimum number of virulence factors necessary for survival in each zone. Since the appearance of strains 21-1 and 21-2 it has been possible to relate the presence of factors for virulence (pathgenes) in the strain to its ability to survive in the field. The pathgenes that have been considered in the relationship are those concerned in the susceptibility of the commercial varieties Eureka and Gabo and the laboratory stocks Kanred and W 1656.* From Figure 5 it is apparent that to certain strains all four varieties are susceptible, to others all four are resistant.

Results so far obtained (Luig and Watson, unpublished) suggest that the virulence of any particular strain on any one of these four varieties is conditioned by at least one recessive pathgene. A strain such as 222-4 would have at least four recessive pathgenes whereas 21-1 would have the corresponding dominant genes for avirulence either homozygous or heterozygous.

When eight of the eleven recorded strains of Figure 5 are examined on the basis of the reaction of the four abovementioned varieties, the classification shown in Table 9 follows. In this table collections from the southern zone are averaged for the four-year period 1955-58 and the averages are graphed in Figure 10. The final column of Table 9 shows that as the host range of the strain widens, the percentage prevalence decreased in an area where no special pathogenic abilities are required. Consequently strain 21-1 predominates.

* A derivative of *Triticum timopheevi*, C. I. 12,632.

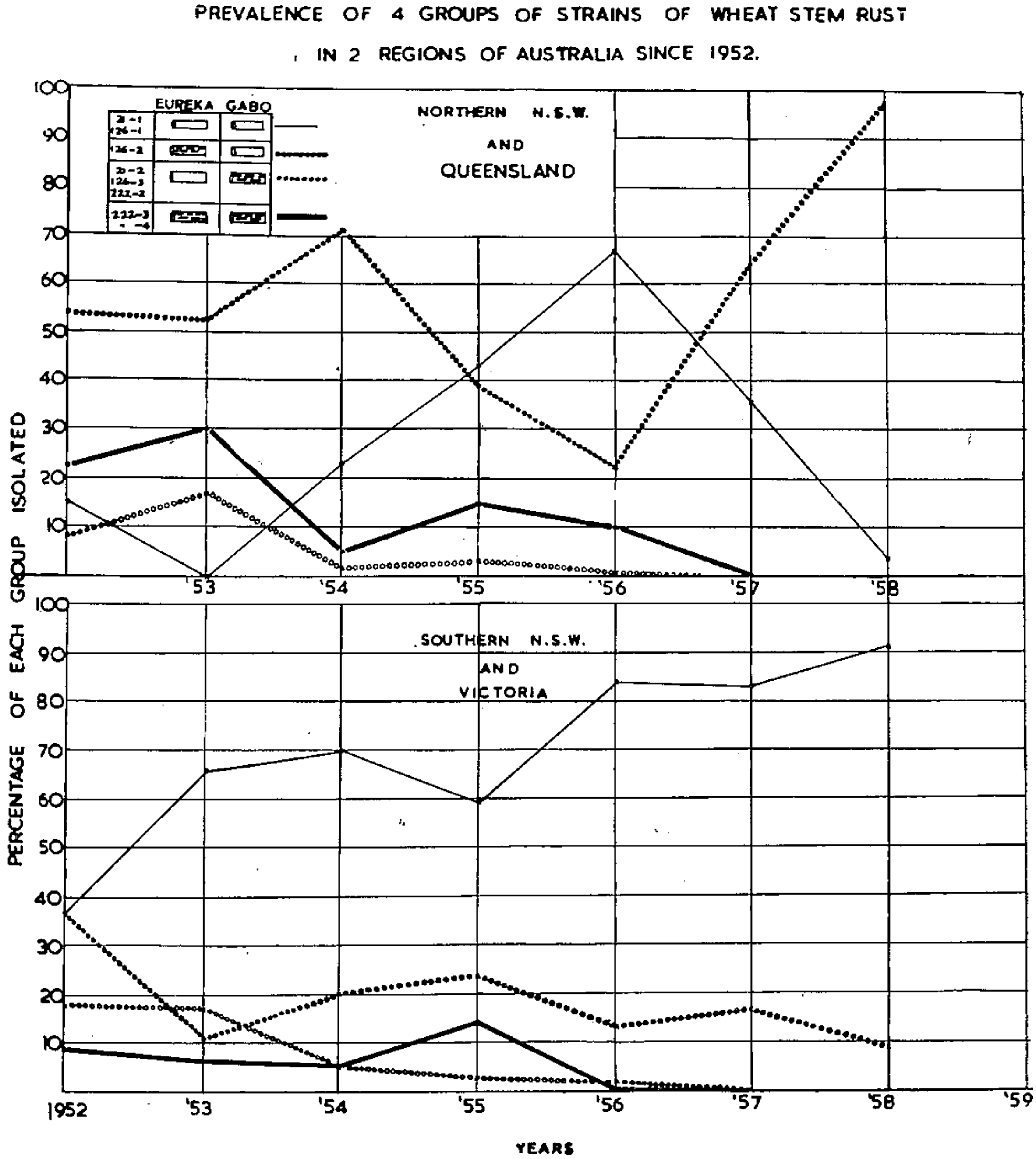

Fig. 9.—Relative prevalence of four groups of strains from 1952 to 1958 in the northern and southern zones of the eastern Australian wheat belt.

This strain has dominant factors for avirulence and these would restrict its development in areas where any of these four varieties are grown. However, they have no deleterious influence on the field survival of this strain in the southern zone where no specific genes for resistance are present in the leading varieties. It therefore has the minimum number of virulence factors necessary for survival.

Strains such as 21-2 and 126-1 each have one recessive factor for virulence, the former for the Gabo-Kenya 745 resistance and the latter for the Kanred immunity. However,

TABLE 9.

Classification of strains of rust in eastern Australia according to their virulence on Kanred, Eureka, Gabo and W 1656 and the frequency of isolation in percent of each group from the Southern Zone.

Group	Reactions	Strains	Frequency of Isolation in Percent
1 ...	All resistant	21—1	61·5
2 ...	3 resistant		
	1 susceptible	21—2, 126—1	10·9[1]
3 ...	2 resistant	126—2, 126—3	
	2 susceptible	222—2	4·2[1]
4 ...	1 resistant		
	3 susceptible	222—3	3·7
5 ...	All susceptible	222—4	0·2

Where more than one strain occurs in a group the percentage frequency of isolation has been divided by the number in the group.

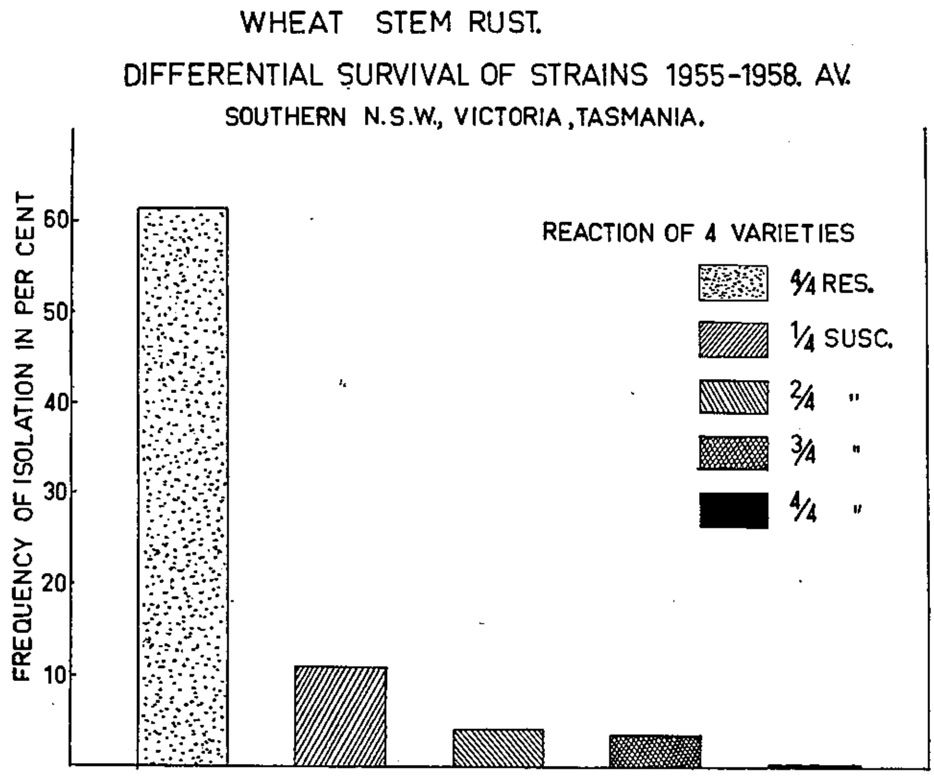

Fig. 10.—Mean relative frequencies for 1955-58 in the southern zone of groups of strains of rust with ability to attack 0, 1, 2, 3, and 4 of the varieties Kandred, Eureka, Gabo and W 1656.

neither of these pathgenes is essential for survival in the southern zone since less than 10 per cent. of the acreage sown is to varieties with either type of resistance (Table 7). On the four critical varieties of Table 9, three dominant genes are present and one recessive in strains of this group. They have a mean of 10.9 per cent. and are second in order of prevalence.

Those strains having genes for virulence on two varieties, namely 126-2, 126-3, 222-3 are next in order with an average of 4.2 per cent. prevalence. These have two more virulence factors than are necessary for sur-

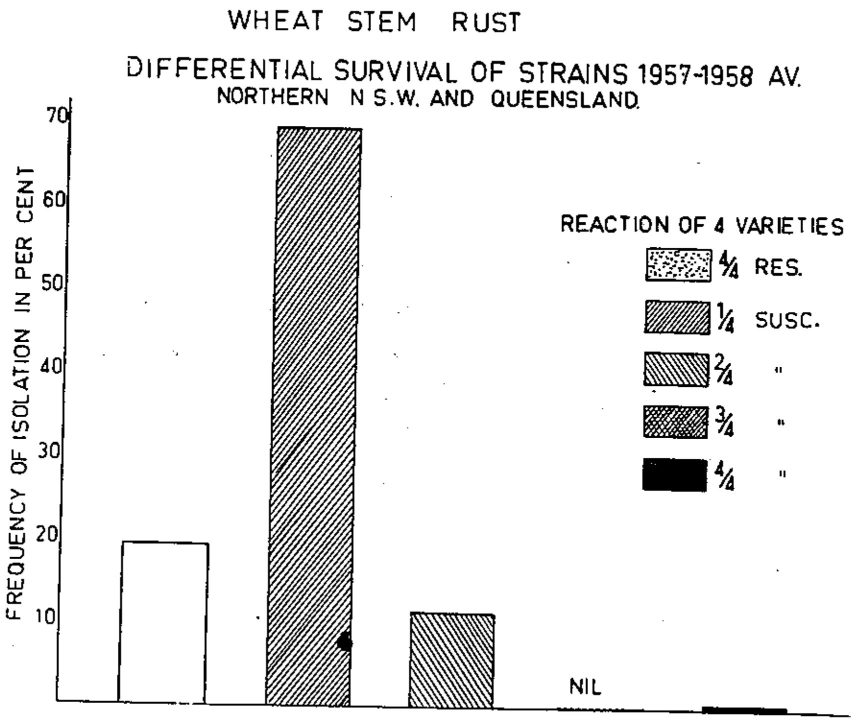

Fig. 11.—Mean relative frequencies for 1957-58 in the Northern Zone of groups of strains with one essential virulence factor associated with different numbers of non essential factors. Strain 21-2 with the minimum number of virulence factors

TABLE 10.

Strains from the Northern Zone grouped according to their number of essential virulence factors and the percentage recovery of the groups from field surveys in 1957 and 1958.

Strain Group	Factors for Virulence		Frequency of Recovery in Per Cent		
	Essential	Non Essential	1957	1958	Average
21—1	0	0	35·7	2·5	19·1
21—2	1	0	46·5	90·1	68·3
126—3, 222—2	1	1	17·8	4·9	11·4
222—3	1	2	......	......	......
222—4	1	3	......	1·2	0·6
Others	......	......	......	1·2	0·6

vival in this zone. Strains 222-3 and 222-4 respectively have three and four genes for virulence over and above the number required. They occur with the lowest average frequency. The accumulation of specific factors for virulence appears to be associated with poor competitive and survival ability and strains having them are unable to become important components of the rust population.

The corresponding results for the northern wheat zones have been given in Table 10 and Figure 11. As shown above, wheats with the Gabo-Kenya 745 type of resistance are widely grown here making up nearly 60 per cent. of the total acreage. To predominate in this zone, strains must have at least one virulence factor which allows them to multiply specifically on the leading varieties. When the strains occurring in this zone are grouped on the four varieties of Table 9 according to their having essential and non-essential virulence factors, the results appear as shown in Table 10.

Strain 21-1 does not have the essential virulence factor and since all four varieties Kanred, Eureka, Gabo and W 1656 are resistant it has no unessential virulence

WHEAT STEM RUST
COMPETITION BETWEEN STRAINS

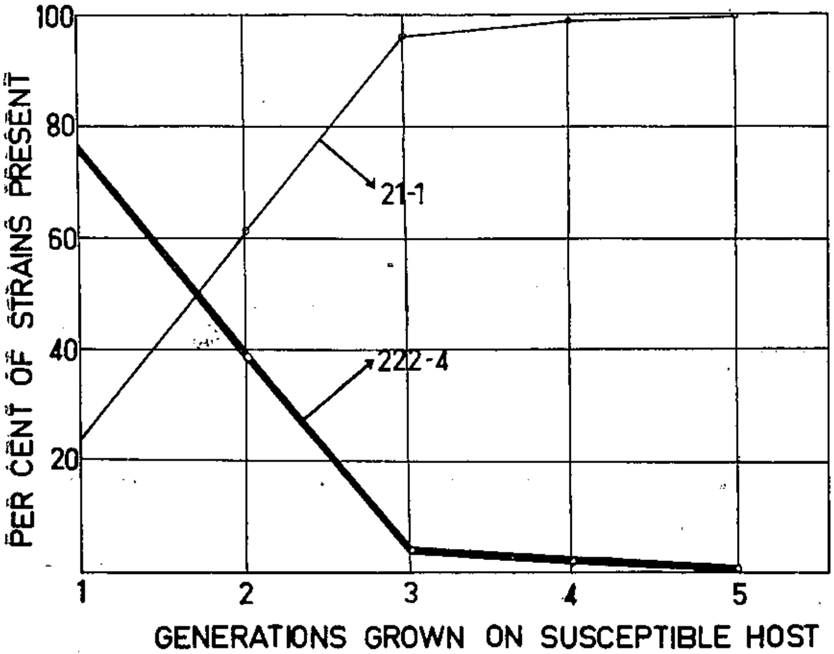

Fig. 12.—Results of growing a virulent strain (222-4) on seedling of Little Club for 5 generations in association with a strain with several avirulent factors.

factors. Strains 21-2, 126-3, 222-2, 222-3 and 222-4 are all pathogenic on Gabo and have therefore the essential virulence factor for survival. This may be associated with all avirulent factors as in 21-2 or with varying numbers of unessential virulence factors.

The fluctuations in percentage prevalence are considerable for the two years 1957-58 and as 21-2 has only been in evidence for this period, no additional years could be tabulated. During this period strain 21-1 decreased from 35.7 to 2.5 per cent. and 21-2 increased from 46.5 to 90.1 per cent. in this zone. Despite the variability, the figures confirm the general principle of survival.

Strain 21-2 with the minimum number of virulence factors predominates in the zone and strains with increasing numbers of unessential virulence factors are least frequent. Those strains with two and three virulence factors are so rare that it is impossible to distinguish between their frequencies over such a short period.

Prior to the occurrence of strains of the 21 group, 126-3 and 222-2 were the predominant types present in the northern zone. Each has the essential factor to attack the Gabo-Kenya 745 resistance but it is associated with a non-essential factor for virulence on Kanred. Since the immunity factor of Kanred has not been incorporated into any Australian variety, these two strains have more than the minimum requirement of virulence factors. Consequently they have been superseded in prevalence by strain 21-2.

It is not clear from the studies so far, why certain strains tend to predominate in the field. According to Stakman and Harrar (1957), no obvious reasons for differential survival have been found. An accumulation of recessive factors for virulence in the pathogen is associated with poor survival. The strain of the organism that accumulates these recessives, becomes so specialised that unless the growth medium (commercial variety) and the environment are such as to swing the balance in its favour it does not maintain itself effectively under field conditions. Khan working at the University of Sydney has studied two Australian strains, 21-1 and 222-4 under laboratory conditions. As shown above, one has a wide host range, the other is avirulent on several varieties.

The results which are given graphically in Figure 12 show that from an original mix-

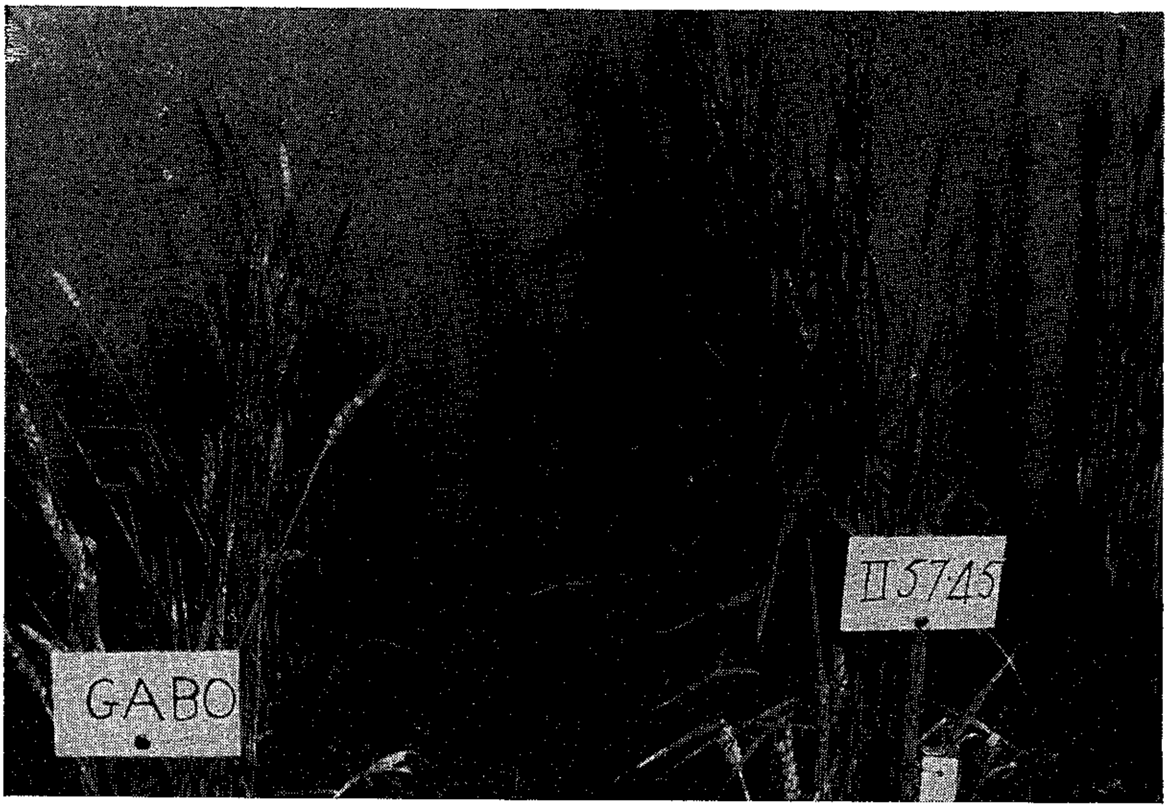

Fig. 13.—Gabo badly damaged by strains 21-2 and 222-4 of stem rust and strains 64-1 and 135-4 of leaf rust. On the right $_2$II 57.45 is the F_1 of a cross (Gabo^7 x Mentana) x (Gabo^2 x Kenya 117A) (Gabo^7 x Mentana) x (Gabo^7 x Eureka x W 1656) showing immunity to all strains of both organisms at Castle Hill, 1958.

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ture comprising 25 per cent. of 21-1 and 75 per cent. of 222-4, only a trace of the latter was recovered after five generations. This has borne out completely the results from field study and Khan has found a number of factors which contribute to differential survival in mixtures.

While the survival of strains of wheat stem rust appears to be inversely correlated with the number of unessential virulence factors, the existence of well defined zones of cultivation has helped to demonstrate it. In few countries of the world would such differences between areas be found. In spite of this, collections of leaf rust from the Gabo and non-Gabo areas have failed to demonstrate the same principle and it is possible that large volumes of wind-blown inoculum have tended to obscure the results. Further detailed work is required before the principle can be applied to the wheat leaf rust organism in eastern Australia.

Synthesis of Stem Rust Resistant Varieties

Several stem rust resistant varieties are cultivated at the present time throughout the wheat belt, but not one of them has the characters suitable for a leading variety.

Glenwari is high yielding and rust resistant, but it produces a grain of inferior quality for bread making purposes. Warigo, with the same source of resistance, has been inconsistent in yield and the grain quality has been unsatisfactory for a wheat adapted to the northern zone.

Spica, another high yielding variety, has an excellent resistance to stem rust but is weak in the straw and the grain, and though of good quality, is hard to thresh. Festival, the leading variety in Queensland, has shown a satisfactory resistance to stem rust, but under New South Wales conditions, it does not yield as well as certain other varieties.

The above mentioned types are being used as parents in further crosses. In addition the resistance shown by the following is being developed in various programmes:—

Webster.—The morphological resistance of this variety has been utilised in Fedweb and it is still effective against all local strains of stem rust. Probably more advantage could be taken of Webster as the nature of the resistance should not be greatly affected by physiological changes in the pathogen.

Eureka and Kenya varieties with Sr_6. The resistance of Eureka, although ineffective against several strains, is still considered valuable for further crosses. Kenya 117A has been used with Eureka as the recurrent parent in a backcross programme to transfer resistance and the combination of these two types of resistance is a very desirable one. The gene in Eureka, which appears to be Sr_6 as determined by Knott (1957) is in chromosome XX and allelic with other genes which appear to be even more effective in the control of certain strains. The variety Bowie, for example, which at low temperatures reacts in the same way as Eureka, is much superior at high temperatures. Consequently, in the field, Bowie shows a higher degree of resistance than Eureka.

Gabo and Kenya 745.—The genes present in these two varieties are allelic and possibly identical. The resistance of Gabo, according to Knott, in crosses with Chinese, behaves as if controlled by two complementary dominant linked genes on chromosome X. In crosses with Federation the resistance to Australian strains is controlled by a single gene, irrespective of whether Kenya 745 or Gabo is the resistant parent. Gabo has been used by Pugsley to derive several common varieties in a reconstituted form. Javelin 48, Dundee 48, Dirk 48, Insignia 49 and others each carry the gene Kcl from Gabo. They are more susceptible than Gabo, however, to strains such as 126-3 and 222-3. Kenya 745 has, in addition, a factor which is known to act against some strains. (Watson 1943.)

Kenya 744, *Kenya* 117A *and Egypt NA*95.—The resistance of these three varieties is allelic and the genes responsible may be identical but they have not been studied in a similar genetic background. The gene controlling the resistance is Sr_9, presumably on chromosome XIII. The three varieties show less resistance to strains 21-1 and 21-2 than to the others, but the reason for this is not clear. It is known from overseas work that Kenya 117A and Egypt NA95 have additional factors for resistance and their phenotype has been given by Knott as Sr_7, Sr_9, Sr_{10}. In the field, since the appearance of strains 21-1 and 21-2, the three varieties mentioned have shown less resistance than previously and this has been reflected in their hybrid progeny. There is some preliminary evidence that the genes of Kenya 117A, other than Sr_9, give some protection against strains such as 21-2.

W 1656 (*C.* 1.12632) *and Timvera* 1308.—Each of these varieties contributes a valuable resistance to all strains except 222-4. To 34-1 and 34-2, the resistance appears to be ineffective at temperatures above 75° F. The resistance in C. 1.12632 is controlled by dominant linked factors in chromosome XIII (Nyquist, 1957).

Khapstein 1451.—The resistance of this variety has been found to be controlled by two factors cumulative in their effect (Athwal and Watson, 1956). While it is a comprehensive resistance giving protection against all strains, it is not as effective as the original parent Khapli. Khapstein has been used in breeding work but so far no varieties have been grown commercially with this resistance incorporated. The chromosomes on which the factors responsible are located has not yet been determined.

Combinations of known types of resistance are at present being made in new lines of wheat bred as commercial varieties or as genetic stocks. Eurga, resulting from the cross Eureka^2 x Gabo, is useful for plant breeders' nurseries since it combines the resistance of Gabo and Eureka and is therefore specific for the presence of strains 222-3 and 222-4. It has been used in these nurseries to assist the spread of these two latter strains which, as shown above, compete poorly with other strains.

Crosses are now under test in which attempts have been made to combine other resistances in pairs. In figure 13, for example, the F1 is shown of a cross between a Gabo derivative with Sr_9 from Kenya 117A and a Gabo derivative with resistance from W1656. Gabo, alongside is seriously damaged by rust. The combination is more resistant than either of the parental lines, since the W1656 component gives high resistance to 21-2 and Sr_9 provides effective protection against 222-4.

Another combination that is valuable results from crossing varieties having the mature plant resistance of Hope with those having Sr_9. The ultimate aim is to bring several resistances together in pairs in order to broaden the genetic basis for resistance. Four that are receiving attention at present are: The mature plant resistance of Hope and the physiologic resistance of Khapstein, W1656 and Sr_9 of Kenya 117A. It will be some time, however, before they will be available together in a background that is adapted for commercial cultivation.

Acknowledgments: Many people have helped in the preparation of this manuscript but thanks are especially due to my colleagues Dr. E. P. Baker, of the University of Sydney, and Mr. N. H. Luig, of the New South Wales Department of Agriculture. Mr. R. W. Fitzsimmons, also of the Department of Agriculture, has helped considerably in the preparation of Tables 5 and 7. Wheat breeders in each of the states have kindly answered questions concerning the progress of their work and the help of all is gratefully acknowledged.

References:

ANONYMOUS, 1952—Wheat Varieties in Australia; Farmer's Bull. 173, N.S.W. Dept. of Agric., 132 pp.

ATHWAL, D. S. and WATSON, I. A., 1956—Resistance to *Puccinia graminis tritici* in Khapstein, a *Vulgare* Derivative of Khapli Emmer; Proc. Linn. Soc. N.S.W., **81**: 71-77.

———. ———, 1957 (*a*)—Inheritance of resistance to wheat leaf rust in Mentana, a variety of *Triticum vulgare;* Proc. Linn. Soc. N.S.W., **82**: 245-252.

———. ———, 1957 (*b*)—Inheritance studies with certain Leaf Rust Resistant Varieties of *Triticum vulgare* Vill.; Proc. Linn. Soc. N.S.W., **82**: 272-284.

BLACK, W., 1957—Incidence of Physiological Races of *Phytophthora infestans* in various countries. Scottish Soc. for Res. in Plant Breeding. Ann. Report (1957).

BORLAUG, N. E., 1957—The Development and Use of Composite varieties based upon the Mechanical Mixing of phenotypically similar lines dedeveloped through Backcrossing; Report Third Internat. Wheat Rust Conf., Mexico D.F., Mexico, 1956.

BROWN, A. M., and JOHNSON, T., 1949—Studies on Variation in Pathogenicity in Leaf Rust of Wheat *Puccinia triticina* Erikss. Can. J. Res. Sect. C., 27: 191-202.

CALLAGHAN, A. R., 1954—Quality in the Australian Wheat Crop; Agr. Gaz., N.S.W. Dept. of Agr., **65**: 416-421, 490-93.

FISCHER, G. W. and HOLTON, C. S., 1957—Biology and Control of the Smut Fungi; Ronald Press Co., New York, 622 pp.

FLOR, H. H., 1956—The Complementary Genic Systems in Flax and Flax Rust; Adv. in Genetics, 8: 29-54.

KNOTT, D. R., 1957—The Inheritance of Resistance to Races 15B and 56 of Stem Rust in a number of Varieties of Common Wheat, with particular reference to the Kenya Varieties; Report Third Internat. Wheat Rust Conference, Mexico D.F., Mexico, March, 1956. Mimeographed.

MCMILLAN, J. R. A., 1935—The Unreliability of Selection in the F_2 for Breeding Wheat Resistant to Flag Smut; Jour. Coun. Sci. Indus. Res. 8: 214-222.

NYQUIST, W. E., 1957—Monosomic analysis of stem rust resistance of a common wheat strain derived from *Triticum timopheevi;* Agr. Journ. 49: 222.

PUGSLEY, A. T., 1945—Breeding for Bunt Resistance in Australian Wheats; Jour. Aust. Inst. Agric. Sci. 11: 28-34.

———, 1953—Backcrossing of wheat for Resistance to Bunt in South Australia; Jour. Exp. Agric. 21: 314-320.

———, 1953—Genetics in the Service of Agriculture; Agr. Gaz., N.S.W. Dept. of Agric. 64: 399-400, 441-442, 478-480.

SEARS, E. R., 1956—The transfer of leaf-rust resistance from *Aegilops umbellulata* to wheat Genetics in Plant Breeding; Brookhaven Sympos. in Biol. No. 9.

STAKMAN, E. C. and HARRAR, J. G., 1957—Principles of Plant Pathology; Ronald Press Co., New York, 581 pp.

VAKILI, N. G. and CALDWELL, R. M., 1957—Recombination of spore colour and pathogenicity between uredial *clones* of *Puccinia recondita* f. sp. *tritici.* Phytopath 47: 536 (abst.).

WATERHOUSE, W. L., 1934—Australian Rust Studies IV. Natural infection of barberries by black stem rust in Australia; Proc. Linn. Soc. N.S.W., 59: 16-18, 1 pl.

———, 1938—II. Some Aspects of Problems in Breeding for Rust Resistance in Cereals; Proc. Roy. Soc. N.S.W., 72: 7-54.

———, 1952—Australian Rust Studies IX. Physiologic race determination and surveys of cereal rusts; Proc. Linn. Soc. N.S.W., 77: 209-258.

WATSON, I. A., 1943—Inheritance Studies with Kenya varieties of *Triticum vulgare* Vill.; Proc. Linn. Soc. N.S.W., 68: 72-9.

———, 1949—Preparing for the occurrence of New Races of Rust. Nature. 163: 730-731.

———, 1955—The occurrence of Three New Wheat Stem Rusts in Australia; Proc. Linn. Soc., 30: 186-190.

———, 1957 (*a*)—Mutation for pathogenicity in *Puccinia graminis* var. *tritici;* Phytopath, 47: 507-509.

———, 1957 (*b*)—Further studies on the production of new races from mixtures of races of *Puccinia graminis* var. *tritici* on wheat seedlings; Phytopath, 47: 510-512.

WATSON, I. A. and LUIG, N. H., 1958 (*a*)—Widespread natural infection of Barberries by *Puccinia graminis* in Tasmania; 'Proc. Linn. Soc. N.S.W., 83: 181-186.

———. ———, 1958 (*b*)—Somatic hybridisation in *Puccinia graminis* var. *tritici;* Proc. Linn. Soc. N.S.W., 83: 190-195.

WATSON, I. A. and SINGH, D., 1952—The future for rust resistant wheat in Australia; Jour. Aust. Inst. Agric. Sci., 18: 190-197.

WATSON, I. A. and WATERHOUSE, W. L., 1949—Australian Rust Studies VII. Some recent observations on wheat steam rust in Australia; Proc. Linn, Soc. N.S.W., 74: 113-131, 2 pl.

———. ———, 1945—A Third factor for resistance to *Puccinia graminis tritici;* Nature, 155: 205.

WENHOLZ, H., 1934—Australian Wheats. The Parentage or Origin of Noteworthy Varieties, Part 1; S.U.A.G.A. No. 15.

Reprinted from the New South Wales Department of Agriculture's Agricultural Gazette, Vol. 69 Part 12, of December, 1958.

Sydney: V. C. N. Blight, Government Printer—1959