THE CLASSIFICATION OF *PUCCINIA GRAMINIS* VAR. *TRITICI* IN RELATION TO BREEDING RESISTANT VARIETIES.

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(Five Text-figures.)

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Synopsis.

A system of classifying strains of *Puccinia graminis* var. *tritici* is outlined and applied to the strains collected in the Australia-New Zealand geographical area. Genes present in the differentials of Stakman and Levine are of limited value in describing the pathogenicity of the common strains of wheat stem rust in Australia. Using these genes, however, in conjunction with those present in six other varieties, an accurate description of the pathogenicity of a particular collection of rust can be given. The varieties used as parents in breeding for stem rust resistance in Australia provide the most useful genes for differentiation. Once a variety becomes widely cultivated the rusts develop an ability to attack it and this results in a close relationship between the area sown to varieties with a particular gene and the frequency of the rust strains against which that gene offers no protection. Probably a broad genetic base on which resistance depends offers a more lasting protection against variability in the fungus.

In an earlier publication dealing with leaf rust of wheat (*Puccinia recondita* Rob. ex Desm.) the authors (1961) outlined the relationship between breeding for resistance to that fungus and the variability that it showed. We indicated the procedure that was adopted in the annual strain survey work conducted, the difficulties in attaining a standardized procedure throughout the world, and finally we suggested a scheme for classification which was based on that used by potato workers for the strains of the Late Blight fungus. This system for leaf rust has proved entirely satisfactory and we now propose to report on the scheme for stem rust which we have had under trial for four years. This report, therefore, will be a companion paper to our earlier work, but will be related entirely to the stem rust fungus, *Puccinia graminis* var. *tritici* Eriks. and Henn. The scheme is not put forward as the ultimate in classification, but we are using it in conjunction with our efforts to breed stem rust resistant wheat varieties. Only differences which are known to be of practical significance for breeding have been considered in the classification, but since we firmly believe in the long-term continuity of these studies and the integration of this work with similar work elsewhere, we have utilized varieties that are well known throughout the world.

While we recognize the races previously described, we do not recognize the term "sub-race" since this involves ranking some host genes as superior to others. Phenotypes that can be separated pathogenically we describe as strains, and they may or may not belong to the same race. Hence we have recorded 25 strains from the field which may be grouped into seven "standard" races.

Earlier Work on Stem Rust.

The classical studies of Stakman and Levine (1922) are so well known that little mention need be made of them here. They selected twelve differential varieties which have become recognized throughout the world as the standard differential series. Collections of rust which are separable on them have been referred to as "standard" races (Stakman *et al.*, 1962).

Waterhouse, in the early stages of the Australian investigations, had access to this material and showed clearly (1929) that the varieties selected in the United States were of value under local conditions for differentiating between the "standard" races of stem rust that occurred in this country. A misconception developed and it was assumed that

race 34 identified in Australia was the same as race 34 in the United States. Waterhouse and Watson (1941) showed that this was not so and that several differences existed between Australian race 34 and United States race 34. In countries throughout the world it is now well known that the "standard" races may comprise many types, and Stakman *et al.* (1962) have discussed much of the background that has developed around this problem.

The significance of differences between components of the "standard" races became evident in 1942 when the variety Eureka carrying the gene Sr6 for stem rust resistance became susceptible. The rust involved, a hitherto unknown strain, was indistinguishable from the predominant strain previously present, except that one attacked Eureka, the other did not. The former was called 126B and the latter 126 (Watson and Waterhouse, 1949). This was the first happening of its kind occurring in Australia and in the absence of barberry infections was not readily explained. However, similar happenings now occur with monotonous regularity in leaf rust (Watson and Luig, 1961) and also in stem rust.

In view of its susceptibility, Eureka was replaced in commercial cultivation by varieties having the gene Sr11[1]. This gene gave protection against "standard" race 126 and the Eureka attacking component 126B, the two types known to be present at the time. Varieties in this group were Gabo, Charter, Yalta, Kendee and Saga. The susceptibility of these in 1948 to new and unrecorded types of rust required a new system of nomenclature. Waterhouse (1952) used the letters A and B to denote avirulence and virulence respectively for a particular variety, e.g., 222AA was avirulent on Eureka (Sr6) and Yalta (Sr11), but 222AB attacked Yalta but not Eureka.

Modifications to this system were made as the variability in the organism became more complex and the lettering was replaced by numbers which were given in order of isolation of the particular rust type in the Australia–New Zealand geographical area, e.g., 126–Anz–1, 126–Anz–2, 126–Anz–3 (Watson, 1955; 1958). While this was satisfactory up to a point, it necessitated the use of a key at note taking and, moreover, it did not convey to wheat breeders the intimate relationship between the virulence of the strain and the resistance of the host. Within the "standard" race 21, for example, the differentiation of at least eight distinct components can be demonstrated by the use of five different genes unlike those present in varieties of the international series. Such complexity has necessitated a search for the most convenient and efficient system of nomenclature.

Rust Collection and Identification.

In order that samples of rust may be obtained from widely separated areas, it has been the practice for several years to send out seed of six varieties sufficient to plant a row six feet long of each. This seed is sent to our co-operators who may be farmers, schoolteachers or agronomists. The varieties are Federation (no known resistance genes), Yalta (Sr11), Eureka (Sr6), Gamenya (Sr9), Mengavi (C.I.12632 resistance) and Black Winter Rye. If rust develops on plants of these varieties from volunteer inoculum, it is forwarded for study. Usually 400–500 samples of stem rust are examined each year and these may come from one or more of the 400 sites where the above varieties are grown or they may come from samples collected in commercial crops. The material is increased on a susceptible variety and when inoculum develops sufficiently it is used to infect simultaneously seedlings of varieties representative of three groups. In the first group are the members of the international series which have been found useful for the classification of the material into "standard" races. These are Reliance, Mindum, Acme, Einkorn and Vernal Emmer. The second group comprises genotypes which will subdivide the "standard" races and they are either commercial varieties or stocks that have been selected or synthesized for the purpose. These are

[1] While Gabo and related varieties were believed to have two linked dominant complementary genes which Knott and Anderson (1956) called Sr11 and Sr12, Sears and Loegering (1961) and Luig (1960) have found this type of resistance to be due to a single factor which we now refer to as Sr11.

McMurachy W 2088 (Sr6), Yalta W 1373 (Sr11), W 2402 (Sr9), W 1656 (C.I.12632), Renown W 2346 and W 2401 (Sr8). The third group is made up of varieties or stocks which are resistant to all local rust strains at present, e.g., Khapstein W 1451, W 2708 (F.K.N. C.I.13154, II50.17), Golden Ball W 1929 and *Agropyron* derivative W 1961. Other varieties such as Celebration are included from time to time, but normally 15 genotypes are inoculated with each collection from the field. Where it is impossible to determine the components when the collection comprises mixed strains, single pustule isolations from the appropriate genotypes are built up and re-examined.

The examinations are made during the spring and summer months mainly when glasshouse temperatures vary from less than 60° F at night to more than 80° F during the day. As the mean temperature rises seedlings generally become more susceptible. However, of the varieties used in differentiation, only Mindum and McMurachy show such extreme variation as to cause errors in classification. Waterhouse (1929) has already indicated that the same culture could be identified as race 34 in the summer and race 56 in the winter, due to the resistance of Arnautka, Mindum and Spelmar at this latter time. The sensitive reaction of varieties having the gene Sr6 is already well known (Forsyth, 1956).

The Differentiation of Strains in the Geographical Area of Australia and New Zealand.

(*a*) *Early Work.*

The work on specialization of wheat stem rust in Australia was commenced by Waterhouse, and he has presented a summary of the findings until March 31, 1951 (Waterhouse, 1952). The 30 years during which these investigations were carried out can be divided conveniently into the pre- and post-Eureka periods. This latter variety was released in 1938 and a virulent strain of rust was first found on it in 1942 with the isolation from Narrabri of strain 126B (Watson and Waterhouse, 1949). From the commencement of the work until 1942 makes up the first period and the second includes the remaining years.

Until Eureka became susceptible there was no necessity for supplemental varieties in separating stem rust. The international series was believed to give all the differentiation required. Consequently, in this first period Waterhouse records the following "standard" races: 11, 33, 34, 43, 44, 45, 46, 54, 55, 56 and 59, and the reaction types are given in the keys prepared by Stakman *et al.* (1962). These "standard" races, with the exception of 34, cannot now be isolated from the field; they have been lost from the culture collection and almost nothing is known of them. From Waterhouse's results (1936), however, it is quite apparent that varieties other than those of the standard series would separate them. It is highly probable that certain Australian varieties used in conjunction with those of the standard series could have been used to give a refinement to the classification of the strains in this first period of study.

The second period which began with the isolation of the strain capable of attacking Eureka is characterized by an increasing complexity in pathogenicity of the components within the "standard" races. Waterhouse (1952) records these latter as 11, 14, 21, 56, 126 and 222, only about half the number recovered in the previous period. However, in 222 he found 222AA, 222AB and 222BB where A and B are used as described above. Eureka attacking strains required the addition of genotypes with Sr6, and the strains virulent on Yalta which were first isolated from Queensland in 1948 required the addition of genotypes with Sr11 for their identification. "Standard" race 34, which is listed as having been found prior to 1942, is not recorded for the second period and presumably it did not occur. It will be shown later, however, that strains of rust are still present both in Australia and New Zealand which collectively conform in their reaction types to "standard" race 34.

(*b*) *Later Work.*

The period we have particularly under review at present commenced in April, 1951, and continued to the present day. There are several outstanding features of the period,

which may be mentioned briefly. Eureka rapidly receded in popularity and it was difficult to isolate strains that were virulent on genotypes with Sr6. The commercial varieties with the gene Sr11, Charter Kendee, Yalta, Gabo and Koda began to lose popularity and this was hastened with the isolation of the virulent and aggressive strain 21–2 in 1956. Festival, a variety with the gene Sr9, gained widespread recognition in northern New South Wales and Queensland, and became the leading wheat in the latter State. Since 1960–61, however, at least two components of "standard" race 21 virulent on it will lead to a reduction in acreage. Spica and Glenwari, two varieties which have a similar type of adult plant resistance, proved popular, but strains were isolated virulent on them. Finally, the period is noteworthy for the release of two backcross derivatives resembling Gabo, Gamenya with Sr9 and Mengavi with a gene from C.I.12632 (Watson *et al.*, 1960). The former has followed the pattern of Festival since they have the gene Sr9 in common, and Mengavi has been damaged in the field by a strain 34–2,4 which appears to be the only one so far in the field to which it is susceptible.

The genes Sr6, Sr11, Sr9 and those from C.I.12632 and Hope have figured largely in the breeding of the rust resistant varieties in Australia. Watson and Luig (1961) have suggested that the classification of the strains of rust in any geographical area is related to the genes for resistance that have been used by the breeders. With the ever-increasing complexity of the pathogenicity pattern of the strains for varieties with these genes, we have been obliged to modify the system of classification. We have given the reasons for doing this with leaf rust and they also hold for stem rust and will not be repeated. An attempt has been made to compromise between a classification that takes account of minute variations between different genotypes of the fungus and in which environment is of extreme importance, and one that is of practical value in a breeding programme designed to control rust in its multiplicity of strains. To do this we have used the varieties of the international series and according to the conventional procedure have isolated "standard" races 17, 21, 34, 40, 116, 126 and 222, the reactions of which agree fairly closely with those of the same number listed in the latest key (Stakman *et al.*, 1962). It is now recognized that these designations are of restricted value and this is particularly evident in Table 1 where there are five components of "standard" race 34 and eight of 21. In separating the components we have made use of the modified potato–*Phytophthora infestans* system as outlined earlier (Watson & Luig, 1961). The supplementals have been numbered to approximate the chronological order in which the genes they contain became available in commercial varieties, hence this arrangement Sr6–1, Sr11–2, Sr9–3, C.I.12632–4, Renown W2346–5 and Sr8–6. The gene Sr8, however, although in a differential variety, has not been used commercially. The letters Anz indicate the geographical area from which we have collected the material.

So far the system has only been applied to material collected in the field. During extensive sexual and asexual hybridizing investigations (Luig & Watson, 1961; Watson & Luig, 1962), we have isolated many strains which are separable both as "standard" races and their components, but these have not so far been catalogued.

The reactions shown in Table 1 are typical of those obtained during the main survey period which extends from September to December. Temperatures are sufficiently low to allow the gene Sr6 to be operative against the particular strains.

Considerable testing was carried out over many years before these varieties were selected to serve as supplementals. The following information about each of the six has been accumulated from our own work as well as from that of others and is presented in order.

1. *McMurachy W 2088 (Sr6).*—The first stem rust resistant variety to be widely cultivated in Australia was Eureka. It was developed from the cross Kenya W 743 (C6040) × Florence × Dundee (Macindoe, 1941). The genetic nature of the resistance was not known at the time of release, but in 1945 Watson and Waterhouse reported that it was genetically different from the two previous resistances that had been found in

Kenya W 744 (C6041) and Kenya W 745 (C6042). Intercrosses between other varieties and Kenya W 743 suggested that the gene present in the latter was common among wheat varieties (Watson and Waterhouse, 1949). Athwal and Watson (1954) designated this gene Ka_1 and Pugsley (1956) found it to be in a number of lines extracted from the International Rust Nursery. Subsequently Knott and Anderson (1956) and Knott (1962) assigned the symbol Sr6 to this gene and classified a number of varieties from Kenya in which it was present either alone or in combination. A list of these varieties with Sr6 is given in Table 2 and McMurachy is among this group. Work done both in Canada and Australia has shown that the gene Ka_1 and Sr6 are the same (Green *et al.*, 1960). Peterson and Campbell (1953) have placed the gene on chromosome XX.

TABLE 1.

Reaction of Six Supplemental Differentials to Stem Rust Strains in the Australia–New Zealand Area.

Strain	1 McMurachy W2088 Sr6.	2 Yalta W1373 Sr11.	3 W2402 Sr9.	4 C.I.12632 W1656.	5 Renown W2346.	6 W2401 Sr8.	Previous Designations. Waterhouse 1952.	Watson *et al.* 1958, 1960.
17–Anz–2	R[1]	*S*	R	R	R	R	—	—
17–Anz–1,2	*S*	*S*	R	R	R	R	—	—
21–Anz–0	R	R	R	R	R	R	—	21–1
21–Anz–2	R	*S*	R	R	R	R	—	21–2
21–Anz–5	R	R	R	R	*S*	R	—	21–4
21–Anz–1,2[2]	*S*	*S*	R	R	R	R	—	—
21–Anz–2,3	R	*S*	*S*	R	R	R	—	—
21–Anz–2,5	R	*S*	R	R	*S*	R	—	—
21–Anz–2,6	R	*S*	R	R	R	*S*	—	21–3
21–Anz–1,2,3	*S*	*S*	*S*	R	R	R	—	—
34–Anz–2	R	*S*	R	R	R	R	—	34–2
34–Anz–6	R	R	R	R	R	*S*	—	—
34–Anz–1,2	*S*	*S*	R	R	R	R	—	—
34–Anz–2,4	R	*S*	R	*S*	R	R	—	34–3
34–Anz–2,5	R	*S*	R	R	*S*	R	—	—
40–Anz–2	R	*S*	R	R	R	R	—	—
116–Anz–2	R	*S*	R	R	R	R	—	—
116–Anz–2,3	R	*S*	*S*	R	R	R	—	—
126–Anz–6	R	R	R	R	R	*S*	126	126–1
126–Anz–1,6	*S*	R	R	R	R	*S*	126B	126–2
126–Anz–2,6	R	*S*	R	R	R	*S*	—	126–3
222–Anz–6	R	R	R	R	R	*S*	222AA	222–1
222–Anz–2,6	R	*S*	R	R	R	*S*	222AB	222–2
222–Anz–1,2,6	*S*	*S*	R	R	R	*S*	222BB	222–3
222–Anz–1,2,4,6	*S*	*S*	R	*S*	R	*S*	—	222–4

[1] R = Resistance. *S* = Susceptibility.

[2] 21–Anz–1,2 was designated previously 21–7 (Watson and Cass-Smith, 1962).

The gene Sr6 is very markedly affected by temperature changes. This was first demonstrated in Canada by Newton, Johnson and Peturson (1940), and R.L.1373 (W 1304), a variety from Kenya that was used, has the gene Sr6 (Table 2). Under Australian conditions from 1938 until 1954 the effect of temperature on the reaction of varieties with Sr6 was not important in the field since the crop normally ripened before high temperature rendered the gene ineffective. However, following the occurrence in 1954 of strain 21–0 and in 1956 of 21–2, it was observed that Eureka was being damaged in the field if maturity was delayed following late sowings. The reasons for the change were clear when seedlings were inoculated in the glasshouse with strains 126–6, 126–1,6, 21–0 and 21–2 and scored for reaction type. At average temperatures of 60° F strain

TABLE 2.

Wheat Varieties Probably with the Gene Sr6.

Variety or Genotype.	Synonyms.	Source of Sr6 Gene.	Reference
Bokveld W 1224	C.12080		Watson, 1955
Bowie C.I.13146	Texas 3708/22, W 2872	Kenya C9906	Luig and Watson, 1961
Sel. 131	Sister strain to Bowie	Kenya C9906	Johnson and Green, 1957
Eureka W 1325	W 1311, P.I.134044, C12502, C.12503, R.L.1534	Kenya C6040	Macindoe, 1941
Eurga W 2032		Eureka	Watson, 1955
E.W.G. W 1818		Eureka	Pugsley, 1952
Frisco W 1411		Kenya C6040	Macindoe and Brown, 1958
Kentana 48	C.I.12921	Kenya C9906	Borlaug, 1957
Kentana 52	C.I.13085; Sel. from Kentana 48	Kentana 48	Knott and Shen, 1961
Kenya 58 F(L)1	W 1487, R.L.1–34–4, E144 (India), C.I.12471	Red Egyptian	Pugsley, 1956; Knott and Anderson, 1956
Kenya 112A	R.L.1–35–4		Pugsley, 1956; Knott, 1962
Kenya 117A C.I.12568	R.L.1–49–64		Pugsley, 1956
Kenya 117.1.5.F(L)	P.I.124742, C10861, W 1482, W 1465, R.L.1377, R.L.1–40–40, Minn. 2696	A.8	Pugsley, 1956
Kenya 122 D.I.T.(L)	W 1304, R.L.1373, Minn. 2693, W 1478, C.I.12186	A.8	Knott and Shen, 1961; Pugsley, 1956; Watson and Waterhouse, 1949
Kenya 130.B.6.B	P.I.117775, C10866, W 1472, R.F.321, W 1473, P.I.118904, R.L.1358, R.L.I/4044		Pugsley, 1956
Kenya 223		Kenya 112	Knott, 1962
Kenya N.B.263J(L)	P.I.117526, C9968, W 1458, R.L.1356, Calif. 3098		Pugsley, 1956; Knott and Shen, 1961
Kenya 291J.1.I.1	P.I.177172, W 1350, R.L.1–48–41	Kenya 58 F(L)1	Pugsley, 1956; Knott, 1957*b*
Kenya 318 A.J.4.A.1	Kenya Ploughman, C.I.12881	Kenya 112	Knott and Shen, 1961
Kenya R.F.324	R.L.1387, C9906, P.I.118896, P.I.117768, C.I.12882, W 1456, Calif. No. 3098, P.I.168699		Pugsley, 1956; Knott, 1957
Kenya 337.V.1.B.1		K.291 or K.223	Knott, 1962
Kenya 337.V.3.A.1		K.291 or K.223	Knott, 1962
Kenya 337.V.3.A.2		K.291 or K.223	Knott, 1962
Kenya 337.V.3.B.1		K.291 or K.223	Knott, 1962
Kenya 341.E.1.A.1		Eureka	Knott, 1962
Kenya 341.F.2.D.1		Eureka	Knott, 1962
Kenya 341.F.2.D.2		Eureka	Knott, 1962
Kenya 341.O.2.B.1	P.I.177183	Eureka	Knott and Shen, 1961
Kenya 344.T.4.C.1.A		Kenya 291	Knott, 1962
Kenya 344.T.4.C.1.C		Kenya 291	Knott, 1962
Kenya 350.AD.9.C.2	P.I.177185	K.223	Knott, 1957*b*
Kenya 350 AJ.3.C.1		K.223	Knott, 1962
Kenya 350.CZ.B.2		K.223	Knott, 1962
Kenya W 1034			Watson and Waterhouse, 1949
Kenya W 1037			Watson and Waterhouse, 1949
Kenya N.B.F6.K2. G6.A.9(L)	W 743, C6040, K2, P.I.124736, R.L.1513, P.I.103539		Knott, 1962; Pugsley, 1956
Kenya A.8			Knott, 1962
Lerma 50	C.I.12981	Kentana 48	Borlaug, 1957
Marquis BC-Line	W 2400	Kenya 58	Green *et al.*, 1960
Mayo 54			Sunderman, 1961
McMurachy W 1488	C.I.11876, R.L.1313, C.12451		Knott and Anderson, 1956; Pugsley, 1956
Moora		Eureka	Macindoe and Brown, 1958
Negroz 11–45			Pugsley, 1957
No. 43	P.I.159106–1*c*, C.I.170915		Pugsley, 1957; Knott, 1957
No. 466–4–M–M–M	P.I.159098		Knott and Shen, 1961
Onas 52		Kenya N.B. 263J(L)	Pugsley, 1957
Red Egyptian C.I.12345			Knott and Anderson, 1956
Red Egyptian type	P.I.170910		Knott, 1957
Selkirk	C.I.13100	McMurachy	Green *et al.*, 1960
Stockade		Eureka	Hore and Sims, 1963
Sweden W 1230	C12266		Watson and Waterhouse, 1949
Travis W 2871			
White Federation 45		Eureka	Pugsley, 1952
Wongoondy W 1746			Macindoe and Brown, 1958

126–6 failed to sporulate, producing only tiny flecks; strains 21–0 and 21–2 on the other hand produced "1‡" reactions. As the temperature increased the onset of complete susceptibility came at a lower temperature with 21–0 and 21–2 than with 126–6. These results on seedlings were correlated with similar results on adult plants in the field.

Differences in the temperature relationships of the strains on homozygous material is also reflected in differences in the dominance relationship of the Sr6 gene. It was shown by Luig (1961) that the F_1 seedlings of the cross Federation × Eureka gave a ";" reaction to strain 126–6 at 60–65° F, but "X" to 21–2 at the same temperature. At 75–80° F the F_1 seedlings give "X" to 126–6, but "3+" to 21–2. The same gene has been found to control the reaction to these two strains. Knott and Anderson (1956) found Sr6 was dominant when resistance to "standard" race 56 was tested, but recessive when the inoculations were made with "standard" race 15 (B). It is not stated whether these differences from the Canadian rusts are reflected in a differential response in homozygous material with Sr6 at varying temperatures such as we have found with strains 126–6 and 21–2.

The value of the gene Sr6 in a supplemental differential is now well established in this geographical area and results of others suggest it is useful elsewhere, although it is not always easy to determine which particular gene is operating in unknown material. In Canada, Johnson and co-workers (1956, 1957) found Sr6 could be used to split components of "standard" race 87. Peturson *et al.* (1960) used this gene to split "standard" races 48 and 56 and Green and Samborski (1961) used it for the same purpose on "standard" races 11, 15 and 29. In the United States it would be expected that the gene would also serve as in Canada for the subdivision of "standard" races, and this appears to be the case from the work of Stakman *et al.* (1962).

In India Sr6 is also useful for the more detailed classification of strains of rust as it is present in the variety E144 which separates the components of "standard" race 42 (Uppal and Gokhale, 1947).

2. *Yalta W 1373 ((Kenya C6042 × Pusa 4) × Dundee).*—The selection from Kenya accessioned as W 745 (C6042) was introduced into New South Wales more than 30 years ago and was used extensively by Macindoe and Waterhouse in the breeding of stem rust resistant varieties. Charter, Kendee and Yalta each derived their resistance from this introduction (Macindoe and Brown, 1958). A study of the genetic nature of this resistance was reported by Watson (1943), and it was found that the same gene conditioned resistance to many "standard" races in the United States as well as to "standard" race 15 from Japan. In extensive crosses Watson and Waterhouse (1949) found this gene to be present in other varieties from Kenya and also in Gabo, a derivative of Gaza, a variety of *Triticum durum*. Subsequent work of a pathological nature, in which many varieties have been tested with strains carrying known genes for virulence, suggests that this gene is common among other varieties of *T. durum* which were introduced to Australia from Greece and Egypt about 1930. Athwal and Watson (1954) listed this gene as Kc_1.

The genetic nature of the resistance of this group of varieties and particularly of Gabo has been confused for some time. At least part of the confusion has resulted from the naming of the variety Timstein which was believed to have come from a cross involving Steinwedel and *T. timopheevi*, but which is in fact a sib of Gabo (Watson and Stewart, 1956; Knott and Anderson, 1956). These authors showed quite independently that Gabo, Timstein and Lee all had the same type of resistance and presumably it had come from Gaza. Earlier, Sears and Rodenhiser (1948) had shown that Timstein had two dominant complementary genes linked on chromosome X. A similar conclusion was reached by Plessers (1954), and Knott and Anderson (1956) subsequently assigned the symbols Sr11 and Sr12 to these two genes. These results for Gabo and Timstein had been obtained using Chinese Spring as the susceptible parent. Work in Australia (Athwal, 1953) and in the United States (Macindoe, 1941) had shown that when Gabo was crossed with certain other varieties as susceptible parents a single gene for resistance to several "standard" races operated.

Kendee W 1405		Kenya C6042	Watson and Waterhouse, 1949
Kenya 112–E–19–J(L)	W 1483, R.L.1873		Watson and Luig, 1961
Kenya 338.AA.1.A.2	P.I.177180		Hayden, 1956
Kenya 338.AC.2.E.2	Kenya Farmer, C.I.12880, P.I.187165, R.L.1–49–89		Hayden, 1956; Pugsley, 1956
Kenya W 745, C6042	G.304–461(C), Kenya Standard, B286		Watson, 1941
Kenya W 1035			Watson and Waterhouse, 1949
Kenya W 1049	R.L.I/35–2		Watson and Waterhouse, 1949
Kenya W 1053			Watson and Waterhouse, 1949
Koda W 2024		Gabo or Kenya C6042	Watson, 1958
Lee C.I.12488	W 2084	Gaza	Watson and Stewart, 1956
Rapier 48 W 1995		Gabo	Macindoe and Brown, 1958
Rhodesian W 1229	C.12272		Watson and Waterhouse, 1949
Ridley 48 W 1998		Gabo	Macindoe and Brown, 1958
Sabre W 2856		Gabo or Kenya C6042	Macindoe and Brown, 1958
Saga W 2031		Gaza	Macindoe and Brown, 1958
Scimitar 48 W 1999		Gabo	Macindoe and Brown, 1958
Seewari 48 W 1996		Gabo	Macindoe and Brown, 1958
Timstein C.I.12347	R.L.2500, W 2006	Gaza	Watson and Stewart, 1956
Winglen W 2855		Kenya C6042	Macindoe and Brown, 1958
Yalta W 1373		Kenya C6042	Watson and Waterhouse, 1949

3. *W 2402 (Kenya 117A × Marquis*[6]; Green *et al.*, 1960*).*—The Australian commercial varieties Festival, Dowerin and Moora owe their resistance to Kenya W 744 (C6041) (Macindoe and Brown, 1958). This latter variety was introduced from Kenya about 1930 and was studied in detail by Watson (1943) and found to have a gene for resistance independent of that present in Kenya W 745 (C6042). The resistance was readily distinguishable from that of Kenya W 743 (Sr6) and Kenya W 745 (Sr11) when seedlings of all three were inoculated individually with the same avirulent strain of rust. Under glasshouse conditions, Kenya W 744 seedlings produce a 3^{-c} reaction and for this reason, in the early stages when Sr6 and Sr11 were so much more effective, they took precedence in the breeding programme.

Studies by Athwal and Watson (1954) showed that in Kenya W 744 and Kenya 117A W 1347 allelic genes were involved in giving resistance to the stem rust in Australia

Two groups of independent workers (Luig, 1960; Sears and Loegering, 1961) have now suggested that a distortion of the ratios occurs in the Timstein and Gabo crosses. Luig, on the one hand, considers that differential transmission of gametes is involved, while Sears and Loegering invoke a killer gene which they suggest is responsible for the removal of certain gametes. It would appear that whatever the basal cause of distortion there is agreement that a single gene is concerned in this type of resistance. As pointed out earlier, we regard this as Sr11.

Sr11 was probably first recognized as a useful supplemental gene in the United States (Watson, 1943). Whereas collections of "standard" race 15 from Japan and the United States were avirulent on Kenya W 745, the gene responsible for giving this protection was ineffective against a collection from Brazil which was subsequently labelled 15B (Loegering and Stakman, 1942).

However, it was not until 1948 that this gene proved useful in Australia, and that was when a new strain of rust on Yalta was collected at Lawes, Queensland. Isolates from the original material showed that two components made up the collection. These were listed as 222AB and 222BB (Waterhouse, 1952). This was the first occasion on which a rust virulent on varieties with the gene Sr11 had been found in Australia. Despite the widespread cultivation of Gabo and other varieties with Sr11 there had been adequate protection until 1948.

In Australia the following commercial varieties have Sr11 as a source of their resistance: Gabo, Charter, Yalta, Kendee, Saga, Winglen, Heron, Javelin 48, Mengavi and Insignia 49. For stem rust strains to be capable of surviving in the areas where these are grown it is essential that they have the virulence factors enabling sporulation to occur. The gene Sr11 under these circumstances becomes important in differentiation. On the North American continent limited use has been made of Sr11 in breeding, and Lee (Hope × Timstein) is the main commercial variety in which it is present. Such restricted use has removed the necessity for the fungus to have virulence on varieties with Sr11 as an essential character for survival. By contrast, in Table 1 it will be seen that the situation in this geographical area with regard to pathogenicity

at that time. They designated the single gene Kb_1. In subsequent studies with Kenya 117A C.I.13140 Knott and Anderson (1956) found three genes, one of which they listed as Sr9. Sears *et al.* (1957) later placed Sr9 on chromosome XIII. Varieties having the gene Sr9 are listed in Table 4.

In a comparison of the reaction of various isogenic lines in Canada and Australia, Green *et al.* (1960) have shown that a line with Sr9 from Red Egyptian reacts

TABLE 4.

Wheat Varieties Probably with the Gene Sr9.

Variety or Genotype.	Synonyms.	Source of Sr9 Gene.	Reference.
Dowerin W 1745		Kenya C6041	Macindoe and Brown, 1958
Egypt N.A.965	C12095, W 1228		Watson and Waterhouse, 1949
Egypt N.A.95	D.I.V.236, P.I.153780, C.I.12894, Kenya A.3, Ux9M.1		Knott and Anderson, 1956
Festival		Kenya C6041	Macindoe and Brown, 1958
Frontana W 1726	R.L.2336, C.I.12470		Knott and Shen, 1961
Gamenya W 2550		Kenya 117A	Watson *et al.*, 1960
Kenora W 2516		Kenya C6041	Macindoe and Brown, 1958
Kenya A.8			Knott, 1962
Kenya K.2			Knott, 1962
Kenya 68		B.286	Knott, 1962
Kenya 73		B256 or B.286	Knott, 1962
Kenya 117A, C.I.13140		A.8	Knott and Anderson, 1956
Kenya 130		K.2	Knott, 1962
Kenya 184.P.2.A.1.E	E581 (India)		Knott, 1962
Kenya 192		K.73	Knott, 1962
Kenya B256.9.1.49.164			Knott, 1962
Kenya 261.R.7.C.1.B		K.68	Knott, 1962
Kenya 261.R.7.C.2.B		K.68	Knott, 1962
Kenya 261.S.10.C.2.D		K.68	Knott, 1962
Kenya 279		K.130	Knott, 1962
Kenya 294.A.N.5.B.3	Kenya Settler	K.117	Knott, 1962
Kenya 294.B.2.A.3	Kenya Settler	K.117	Knott, 1962
Kenya 321.B.T.1.B.1	P.I.177179	K.117	Knott, 1957*b*, 1962
Kenya 321.A.O.1.C.3		K.117	Knott, 1962
Kenya 334.AD.1.D.1			Knott, 1962
Kenya 334.A.D.1.D.3			Knott, 1962
Kenya 338.AA.1.A.2	P.I.177180		Knott, 1962
Kenya 338.AC.2.E2	Kenya Farmer, P.I.187165, C.I.12880, R.L.1–49–89	K.192	Knott, 1957; Pugsley, 1956
Kenya 338.AO.2.C.5			Knott, 1962
Kenya 339		K.192	Knott, 1962
Kenya 344.AD.1.B.1		K.279	Knott, 1962
Kenya 344.AD.1.D.2		K.279	Knott, 1962
Kenya 344.AD.3.D.2		K.279	Knott, 1962
Kenya 344.AD.3.B.1		K.279	Knott, 1962
Kenya 356		K.192 or K.184	Knott, 1962
Kenya 357		K.294 or K.184	Knott, 1962
Kenya 358		K.294 or K.184	Knott, 1962
Kenya 360		K.294 or K.184	Knott, 1962
Kenya 367		K.184	Knott, 1962
Kenya C6041	W 744		Athwal and Watson, 1954
Kenya Standard B.286	P.I.124738, W 2068, P.I.92473		Knott, 1957*b*
Magnif G	P.I.197663		Knott and Shen, 1961
Marquis BC Line	W 2402	Kenya 117A	Green *et al.*, 1960
Moora		Kenya C6041	Macindoe and Brown, 1958
No. 466			Knott and Shen, 1961
P.I.60599			Knott and Shen, 1961
Red Egyptian Type P.I.170910			Knott, 1957
Red Egyptian C.I.12345	R.L.2061		Knott and Anderson, 1956
Rio Negro W 1788	P.I.168687 C.I.12469, E952 (India)		Knott and Shen, 1961
Simpson Rongai 1–49–157			Knott, 1962
Simpson Rongai 1–49–158			Knott, 1962
Simpson Rongai 1–49–159			Knott, 1962
Veadeiro P.I.192475			Knott, 1957

genetic mechanism operated against these strains to confer resistance on seedlings as well as on adult plants. Moreover, it was found that the variety Spica (Three Seas × Kamburico) × (Pusa 4 × Flora) which in 1954 was the leading variety in Queensland was reacting in a way identical with Hope and the Hope derivatives when seedlings were inoculated with strains 126–6 and 21–0. As the leaf rust reaction of Spica parallels that of Renown W 2346 (Watson and Luig, 1961) the pedigree as listed by Macindoe and Brown (1958) is called into question. Evidence from both the leaf rust and the stem rust reactions suggests that either H–44 or Hope has entered into its pedigree. This has considerable significance as will be shown later.

During the 1955–6 epidemic which was caused mainly by strain 21–0 (Watson, 1958) Glenwari showed outstanding resistance and this feature was responsible for its rapid gain in popularity in subsequent years. It was, however, developed for cultivation

TABLE 6.

Summary of the Number of Isolations of the various Strains grouped according to the Year of Collection.

Strain	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963*	Total.
17–Anz–2..	—	—	—	—	—	—	—	—	—	—	2	3	5
17–Anz–1,2	—	—	—	—	—	—	—	—	—	—	—	3	3
21–Anz–0..	—	—	—	42	234	192	19	22	68	7	10	8	602
21–Anz–2..	—	—	—	—	—	64	85	484	464	373	390	166	2026
21–Anz–5..	—	—	—	—	—	—	—	—	41	34	115	112	302
21–Anz–1,2	—	—	—	—	—	—	—	—	—	—	15	134	149
21–Anz–2,3	—	—	—	—	—	—	—	—	—	4	156	239	399
21–Anz–2,5	—	—	—	—	—	—	—	—	—	—	2	5	7
21–Anz–2,6	—	—	—	—	—	—	—	1	—	1	1	1	4
21–Anz–1,2,3	—	—	—	—	—	—	—	—	—	—	33	72	105
34–Anz–0..	—	—	—	—	—	—	—	—	—	—	7	—	7
34–Anz–2..	—	—	—	—	—	—	2	43	106	37	157	114	459
34–Anz–4..	—	—	—	—	—	2	—	1	—	—	—	—	3
34–Anz–1,2	—	—	—	—	—	—	—	—	—	—	—	10	10
34–Anz–2,4	—	—	—	—	—	—	—	—	1	1	31	299	332
34–Anz–2,5	—	—	—	—	—	—	—	—	—	—	—	3	3
40–Anz–2..	—	—	—	—	—	—	—	—	—	—	1	1	2
116–Anz–2..	—	—	—	—	—	—	—	—	—	—	—	2	2
116–Anz–2,3	—	—	—	—	—	—	—	—	—	—	10	17	27
126–Anz–6..	49	14	32	116	84	15	4	12	56	12	2	—	396
126–Anz–1,6	22	7	1	14	8	—	—	5	—	—	2	2	61
126–Anz–2,6	—	—	5	5	39	35	3	5	2	—	—	—	94
222–Anz–6..	1	—	4	11	—	—	—	11	36	3	—	—	66
222–Anz–2,6	10	14	28	86	39	9	1	—	—	—	—	—	187
222–Anz–1,2.6	4	9	4	40	13	—	—	—	—	—	—	—	70
222–Anz–1,2,4,6 ..	—	—	—	1	—	—	—	—	—	—	—	—	1
Total	86	44	74	315	417	317	114	584	774	472	934	1191	5322

* Incomplete.

in the southern areas not so liable to rust damage and consequently was not exposed to infection by mutants and asexual recombinants which could be expected to occur under epidemic conditions in northern New South Wales and Queensland. It is known from the survey work in Queensland that in 1954–5 strain 21–0 was collected from three locations, from seven locations in 1955–6 and also from seven in 1956–7, but there was no evidence that Spica was susceptible although seedlings were not tested with field collections. However, during the 1957–8 survey period Mr. J. Bligh forwarded Spica damaged by stem rust. Examination of this material showed that it was avirulent on varieties with Sr6, Sr9 and Sr11, but seedlings of Spica, H–44 and Hope derivatives were susceptible. From surveys conducted in New South Wales it was apparent that this strain also occurred on adult plants of Glenwari.

It is apparent from Table 6 that the prevalence of strain 21–0 has declined over the country as a whole, and in Queensland it has not been recovered in the last three years. However, the Spica attacking strain 21–5 has become more abundant and is aided by the cultivation of Gala (Gabo × Lawrence) as well as Spica. During 1961–62

this strain oversummered commonly and late sown crops of Spica suffered damage which was almost entirely due to strain 21–5. Despite the susceptibility of adult plants of Spica to this strain the variety is not normally damaged by stem rust. The early maturity and possibly a degree of tolerance enable it to escape in most years.

It has been pointed out previously (Watson, 1958) that strains of rust lacking the gene for virulence on varieties with Sr11 have difficulty in surviving in the northern areas of the eastern wheat belt where this gene has been responsible for the main protection against rust. However, since this gene has become ineffective, farmers have sought genetic diversity and have grown Glenwari, Gala and Spica in close proximity to varieties such as Gabo and Koda. Mutants arising on the first three may have the opportunity to spread to the latter two and vice versa. Although we have not been able to trace the sequence of events we have collected from Glenwari and varieties with a similar resistance growing in these areas strains 21–2,5 and 34–2,5 which are able to attack varieties with Sr11 or those in which this gene is combined with that giving the Hope type of resistance.

Although Renown is listed in Table 1 as being resistant to strains occurring before 1954, such as 126–6 and 126–1,6, seedlings are susceptible to these strains. Only those strains to which adult plants of Glenwari and Spica are susceptible are shown as virulent on Renown in this table. Such strains are 21–5, 21–2,5 and 34–2,5. So far no strain having the general characteristics of the pre-1954 strains has been found on adult plants of the Renown group of varieties.

Studies on the mode of inheritance of the resistance in seedlings of Spica by Luig (1961) have shown that a single factor is involved and that this factor is the same as that concerned in giving resistance to adult plants to the same strains. The relationship between this resistance and that which protects adult plants against strains to which their seedlings are susceptible has not been determined. Sears, Loegering and Rodenhiser (1957) found two chromosomes, VIII and XVII, to confer resistance to one North American strain each, and the adult plant resistance of Hope was considered to be the result of interaction of genes on different chromosomes, possibly III and XVII. Campbell and McGinnis (1958), however, located three dominant, complementary factors for adult plant resistance to race 56 on chromosomes III, VIII and XIII.

6. *W 2401 (Red Egyptian* × *Marquis*; Green *et al.*, 1960*)*.—The variety Mentana W 1124, introduced into Australia from Italy, has been a valuable source of resistance to leaf rust (Watson *et al.*, 1960), but in the breeding for resistance to stem rust in this country it was not considered as a source of resistance. All the strains common in the field prior to 1954 were virulent on Mentana. However, in 1954–55 a set of characters new to the Australian rust strains became evident when strain 21–0 was isolated (Watson, 1961). Whereas Mentana was susceptible to strains such as 126–6, 126–1,6 and 222–2, it gave a reaction of "2" or "2+" to strain 21–0 and under higher temperatures of the summer these reactions developed into a "3–c". In 1954 the above strain was the only one known to give such a reaction on Mentana, but since that time Watson (1961) has suggested that other strains have arisen from it, either by mutation or somatic recombination, so that all post-1954 strains with the exception of 21–2,6 show the reaction on Mentana characteristic of 21–0. This type of resistance is quite unsatisfactory for protecting adult plants in the field and this variety under an epidemic of strain 21–2, for example, would be classed as susceptible.

When seedlings of Mentana were found to be resistant to field strains, all collections were used to inoculate them as a matter of routine. As a result a collection of rust from Inverell was identified in 1959–60 as 21–2,6. It gave reactions typical of 21–2, but in addition it attacked Mentana. Since 1959–60 it has been isolated on only three occasions.

Since the Marquis backcross lines became available from Dr. D. R. Knott (Green *et al.*, 1960), each has been investigated as having possibilities for making the classification of strains more precise. W 2401, which has the gene Sr8 from Red Egyptian, has been found to react to field strains in the same way as Mentana. Although

the appropriate crosses have not been made we have concluded that one of the genes in Mentana is Sr8. The latter is known to have a single incompletely dominant gene which controls the semi-resistant reaction of seedlings to strain 21–2 (Luig, 1961). This gene was rendered ineffective when an orange culture of strain 21–2 was treated with ultra-violet rays and three independent mutants were found each attacking Mentana. Whereas W 2401 was resistant to the parental culture of 21–2, it, like Mentana, was susceptible to the mutants. We are using W 2401 in preference to Mentana since the latter is known to have other sources of resistance which give a very sharp hypersensitive reaction to certain strains (Luig, 1961; Watson & Luig, 1962). The gene Sr8 has no significance in commercial varieties in Australia at present and it is of limited use in the separation of the components of "standard" races. In both North and South America this gene is probably of considerable value in this connection, as shown by the tables in Green *et al.* (1960) for "standard" race 32 and by the work of Rojas (1957) for "standard" race 15 in Peru. According to Sears *et al.* (1957) the gene Sr8 is on chromosome VI.

Other Differentials being Developed.

In the production of the Marquis backcross lines Knott has made a useful contribution to the simplification of the genotype concerned in stem rust resistance. However, the background contributed by Marquis itself gives some protection against a number of "standard" races, and Knott (1962*b*) has experiments under way to remove this resistance from the background genotype. To several of the avirulent strains which we have produced by somatic recombination and selfing (Watson & Luig, 1962, and unpublished) Marquis shows extreme hypersensitivity and we have found Little Club to be much more desirable in providing a uniformly susceptible background. However, it is agronomically quite unsuitable for Australian conditions, being very late in maturity, and work is in progress to derive earlier maturing lines susceptible to the avirulent strains.

Studies in avirulence of wheat stem rust are coupled with those concerned in inbreeding rye stem rust (Watson & Luig, 1962*b*) while selecting for virulence on wheat. To all cultures of rye stem rust we have found Marquis highly resistant and Little Club mostly gives "2" and "2–" reactions. Material from crosses between wheat varieties has been inoculated with this latter fungus and from an F_2 population of the cross (Little Club × (Gabo^2 × Charter)) a single plant progeny has been developed. This line W 2691 is earlier maturing than Little Club, is as susceptible as the latter to the avirulent strains of wheat stem rust, but much more susceptible to rye stem rust and fully susceptible to those inbreds we have developed by selfing rye rust on barberry (Watson & Luig, 1962*b*). We are now making further selections in W 2691 and using it as a recurrent parent with varieties carrying known genes as donors. We anticipate that such lines will be suitable for the differentiation of strains of both wheat and rye stem rust.

Strain Prevalence in Relation to the Genetic Constitution of the Varieties Cultivated.

When comparing the results of the present survey period with those of the previous ten years recorded by Waterhouse (1952), the most striking feature is the great diversity of strains among the present-day rust population both on the standard and the supplemental differential varieties (Tables 5, 6). Obvious changes in the strain pattern from 1942 to 1951 had taken place as the products of breeding programmes began to be utilized commercially. Strain 126–6 was the prevalent one in 1941, and in 1942 the first two isolations were made of the Eureka attacking strain 126–1,6. Throughout the next 5–6 years there was a general tendency for strain 126–1,6 to build up in prevalence at the expense of 126–6, and this was largely correlated with the increasing acreage sown to Eureka in the rust liable areas (Watson, 1958). Late in 1948 two strains were collected and named 222AB (=222–2,6) and 222BB (=222–1,2,6). These were both virulent on Gabo and related varieties with Sr11, and as these latter were becoming

increasingly popular these strains had a congenial medium on which to grow. The prevalence of strains attacking varieties with Sr6 or Sr11 was in each instance related to the varietal acreage pattern (Watson, 1958; Figs 1 and 2).

The earliest and most significant change to become evident in the present period was the rise in prevalence of rusts having the pathogenicity pattern of "standard" race 21. The origin of this latter is not known, but it seems to have developed from the southern part of the country. Waterhouse recorded it from Kosciusko in 1948 and in 1954–5, when our first isolations were made, it was concentrated in the south of New South Wales, in Victoria and Tasmania. There is a distinct possibility that it had its origin on barberries in Tasmania. The first component to be isolated was 21–0 (Watson, 1955), an aggressive but relatively avirulent strain, and one to which all six of the supplemental varieties were resistant. However, either by mutation or somatic hybridization (Watson and Luig, 1958) there has been a progressive accumulation of abilities in components related to 21–0 and the changes reveal something of the plasticity of this fungus even when the possibility of sexual hybridization is removed. The difficulties involved in breeding a rust-resistant variety are plain.

The eight strains of the 21 series have retained many of the basic characters which first showed up in 1954 to differentiate 21–0 from previously existing strains. These characters have been listed previously (Watson, 1961). From the isolations in the field it would appear that new pathogenic abilities have been added step by step to overcome each new barrier the plant breeder has placed in the way of the fungus. The occurrence of strain 21–2 in the northern areas to overcome the gene Sr11 has already been mentioned. Its origin from somatic hybridization has been demonstrated in the laboratory (Watson & Luig, 1958). Strain 21–5 was found as a variant attacking Spica, Glenwari, Gala and Warigo, all varieties which appear to have the same type of resistance.

The appearance of strains virulent on varieties with Sr9 is clearly related to the increase in their acreage (Fig. 3). Festival increased in acreage from 13·7 per cent in 1955–56 in Queensland to 43·2 per cent in 1960–61 and with the release of Gamenya in 1958 both varieties with Sr9, strain 21–2 the prevalent one was obviously restricted. Strain 21–2,3 was collected on Festival in 1959 first in the Brookstead area of Queensland and is identical with 21–2 except for the additional ability of virulence on varieties with Sr9. As seen from Table 6, it comprised about 20 per cent of the inoculum in the season 1962–3 over the whole country, but was much more concentrated in the areas where Festival and Gamenya are grown (Table 5). In 1961–62 it did extensive damage to late sown crops of Festival in Queensland.

Prior to the isolation of strain 21–2,3 testing had been proceeding with selection 1131, a line originating from the co-operative work with Mr. E. M. Matheson of the State Department of Agriculture. This line closely resembled Festival, but was higher yielding, more resistant and was considered to have the genes Sr6 and Sr9 combined. Whereas Festival was rusted during the summer of 1960–61 at "Anchorfield", Brookstead, Queensland, selection 1131 was resistant. From late maturing plants along the border of the plot, however, Mr. J. E. Bligh collected rust which was identified as strain 21–1,2,3. This was the first case in Australia of a strain attacking varieties with the genes Sr6, Sr9 and Sr11 combined. This strain is widespread in New South Wales, but so far has not developed to epiphytotic proportions. It is the only local strain which is found on Kenya Farmer.

The origin of strain 21–1,2,3 is not known, but it may be connected with the almost simultaneous isolation of strain 21–1,2 from northern New South Wales. This latter is extremely pathogenic on Eureka and similar varieties which in the past were protected by Sr6. It had been found as a rare strain in New South Wales, and in Western Australia it was first recovered in 1961–2 (Watson & Cass-Smith, 1962). In 1962–63 it was the predominant strain in that State devastating crops of Eureka in the Esperance Bay area (unpublished). The extent of the damage was equivalent to any suffered by Eureka from strain 126–1,6 in earlier years and illustrates the importance

of evolution of this special pathogenic ability. In the eastern States Eureka receded in popularity on account of its rust susceptibility from 1946 onwards (Fig. 1). At the peak of its production it was sown on 219,295 acres in the northern wheat zones and occupied 19·2 per cent of the area. By 1955–56 in the same zones this had fallen to 5,641 acres, representing only 0·06 of the total. In plots, however, the high yielding ability of Eureka again became evident as strains virulent on it became very rare (Watson, 1958). In 1957 and 1958 (Table 6) no strains virulent on Eureka were found and for all practical purposes it became a resistant variety. Although it was known that the resistance conditioned by Sr6 could become ineffective at high temperatures, it was recommended that farmers again sow Eureka, but not in late plantings (Walkden-Brown, 1959). Following this advice there was an immediate increase in the area planted and in 1960–61 this represented 111,626 acres or 4·2 per cent of the total plantings in the north of New South Wales. Although this did not reach the 19·2 per cent of earlier years it was a sufficient increase to place a severe selection pressure on the organism, and although later statistics are not available the area probably continued to rise in the two years subsequent to 1960–61. This increased acreage has given us the opportunity to search for mutants and asexual recombinants on Eureka (Fig. 1). Four strains with virulence on varieties with Sr6 at low as well as high temperatures have been found as shown in Tables 5 and 6. These are 17–1,2, 21–1,2, 21–1,2,3 and 34–1,2. The old strain 126–1,6 collected first in 1942 occurs rarely in the north-western areas of New South Wales, but apparently has persisted throughout the past 20 years.

The Eureka attacking strains of 1962–3 are very unlike those of 1942–3. They each combine the basic characters of the "standard" race to which they belong and have certain new characters typical of the post-1954 strains which separate them from 126–1,6. Strains 21–1,2 and 21–1,2,3 are identical with 21–2 and could have arisen from it by stepwise mutation. The virulence for Celebration shown by the original 21–0 is retained. Strain 17–2 appears identical with 21–2 except for its virulence on Einkorn; 17–1,2 only differs from 17–2 in the ability to attack varieties with Sr6.

Strain 34–2 arose about the same time as 21–2. It differs from 21–2 on Reliance as well as Celebration and is possibly a somatic recombinant with 21–2 as one parent. However, one strain, 34–1,2, is also virulent on varieties with Sr6 avirulent on Celebration and has thus retained the characters of strain 34–2. Hence it would appear that the modern strains have acquired this new ability for virulence on varieties with Sr6 as it was required. It would appear that this has been done quite independently of the previous Eureka-attacking strains. Moreover, they have simultaneously inherited, probably from strain 21–0, genes for aggressiveness which have enabled them to overrun strain 126–1,6 completely in the areas where Eureka has been traditionally grown for 20 years.

It has been of considerable interest to find that strains which conform to "standard" race 34 have been recovered during the survey period. Waterhouse (1929) found race 34 in the early stages of his investigations. However, in 1949 Watson and Waterhouse reported that the rust that was then prevalent conformed more closely to "standard" race 126 than to 34. The characters of the former that are clearly recognizable are the mesothetic reactions on Kubanka and Acme and the avirulence at low temperatures on Arnautka, Mindum and Spelmar. All strains of the "standard" race 126 series are avirulent on Celebration and virulent on Mentana. Those of the 34 series are avirulent on Celebration but are differentiated on Mentana.

One of the first strains to be isolated which conformed to "standard" race 34 was 34–2 collected in 1957–58 at Castle Hill and Tamworth. It was thought to be a somatic hybrid between two strains since it combined the characters of virulence on Reliance with avirulence on Mentana and Celebration, the latter character being present in the pre-1954 strains. Strain 34–2 and other strains which conformed to the reactions of "standard" race 34 were examined to determine the relationship between them and strain 126–6. In Table 5 it will be seen that the relatively avirulent strains 34–0 and

34–6 have been recovered only from New Zealand. At high temperatures the latter approximates to 126–6, but at temperatures of 55° to 60° F it is still virulent on Mindum and does not give a mesothetic reaction on Kubanka and Acme. However, it is avirulent on Celebration. Strain 34–0 resembles it closely, but is avirulent also on Mentana. We have been unsuccessful in repeated attempts to locate the type of rust that was originally described by Waterhouse as "standard" race 34, and it must now be assumed that it does not occur in this geographical area.

Strain 34–2, which in recent years has been prevalent in the field throughout a wide area of the country, is a member of a group of four strains of the 34 series, all four being of economic importance. The other three are 34–1,2, 34–2,4 and 34–2,5. Since all these have avirulence on Celebration we believe they have arisen from 34–2 as a parent and have gained virulence on Eureka, C.I.12632 and Renown respectively.

The circumstances under which strain 34–2,4 was first collected, as well as its pathogenicity, have suggested to us the mode of origin of this strain. In May, 1959, it was collected by Mr. J. Bligh on a single culm of Mengavi at Brookstead, Queensland, adjacent to plants of other material rusted by strain 34–2. It was not collected again for 18 months despite searches over many areas of Mengavi crops. In October, 1961, it was collected for the first time in New South Wales. The infected culms with isolated large pustules were infrequent and occurred in an outside row of Mengavi where reduced competition had delayed maturity. Some 10–12 inches away was the outside row of a crop of Winglen badly damaged by strain 34–2. Contiguous rows of susceptible and resistant varieties arranged in this way are probably ideal for the isolation of mutant or recombinant strains and this possibly explains the origin of 34–2,4.

Statistics for the acreages sown to Mengavi in New South Wales are not available, but those for Queensland show a rapid increase in the area sown with this variety (Fig. 5), and we estimate that the combined area was approximately one million acres from the seed produced originally on a row of 50 plants sown in January, 1958. During the years of multiplication the strain 34–2,4 also increased, but at a disproportionate rate relative to other strains because commercial areas sown during the summer months enabled large volumes of inoculum to be available for the infection of the autumn sown crop. As shown in Table 6, a total of only 33 isolations of strain 34–2,4 had been made from April, 1959, to March 31, 1962, from a total of 2180 isolations. During the same period in Queensland there were seven isolations of 34–2,4 from a total of 222. However, for the period April 1, 1962, to March 31, 1963, 99 isolations from a total of 201 in Queensland have been of strain 34–2,4. The strain is confined mainly to northern New South Wales and Queensland, but it made up about 25 per cent of all inoculum examined from the country in 1962–63.

The other strains listed in Table 5 do not appear to have any relationship to the commercial varieties of wheat grown. Strain 17–2 and 17–1,2 are identical with 21–2 and 21–1,2 except for the Einkorn susceptibility to 17–2 and 17–1,2. They are not common in the field and are collected as isolated pustules on Einkorn where epiphytotics are severe in other varieties. Strains 116–2 and 116–2,3 have been isolated from Queensland and northern New South Wales and have the added ability for virulence on Vernal Emmer. Strain 40–2 is too rare at this stage to give any indications of its possible significance.

In the preparation of Figures 1–5, which together give a clear picture of the relationship between the acreage of varieties possessing a particular gene for resistance and the frequency of rust strains unaffected by the presence of this gene, it has been necessary to estimate certain of the acreages since statistics are not yet available. The general trend has not been altered when these estimates are used, but one or two explanatory comments are needed.

Northern New South Wales (the area north of the Great Western Highway) and Queensland can, for purposes of survey work, be regarded as one ecological area, although the variety acreage pattern in the two States may vary somewhat. A close relationship exists between the strains of rust collected in the two areas. In Figure 2

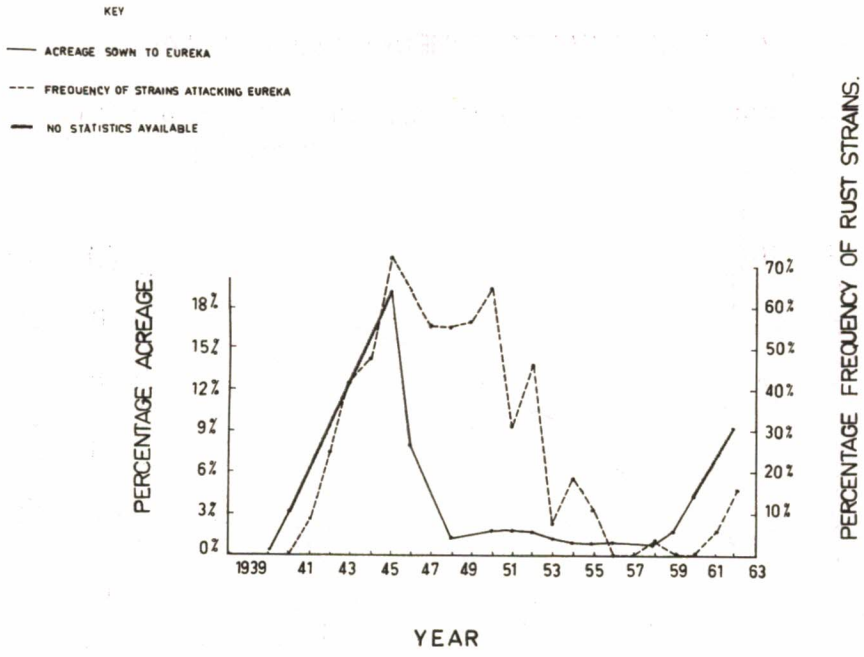

Fig. 1. The relationship between the percentage of the acreage sown to Eureka in northern New South Wales and the percentage frequency of the strains attacking it in northern New South Wales and Queensland.

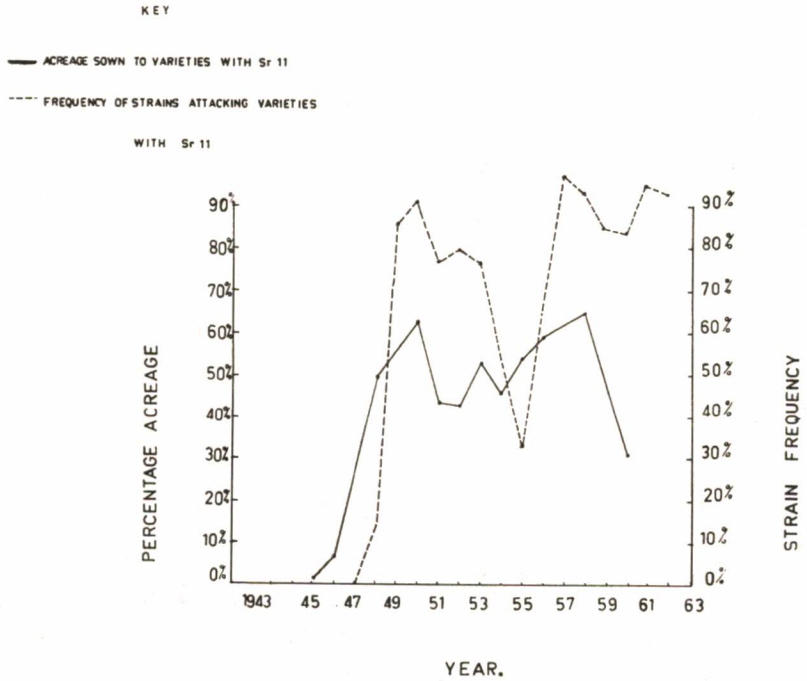

Fig. 2. The relationship between the percentage acreage sown to varieties with the gene Sr11 in northern New South Wales and the percentage frequency of strains attacking them in northern New South Wales and Queensland.

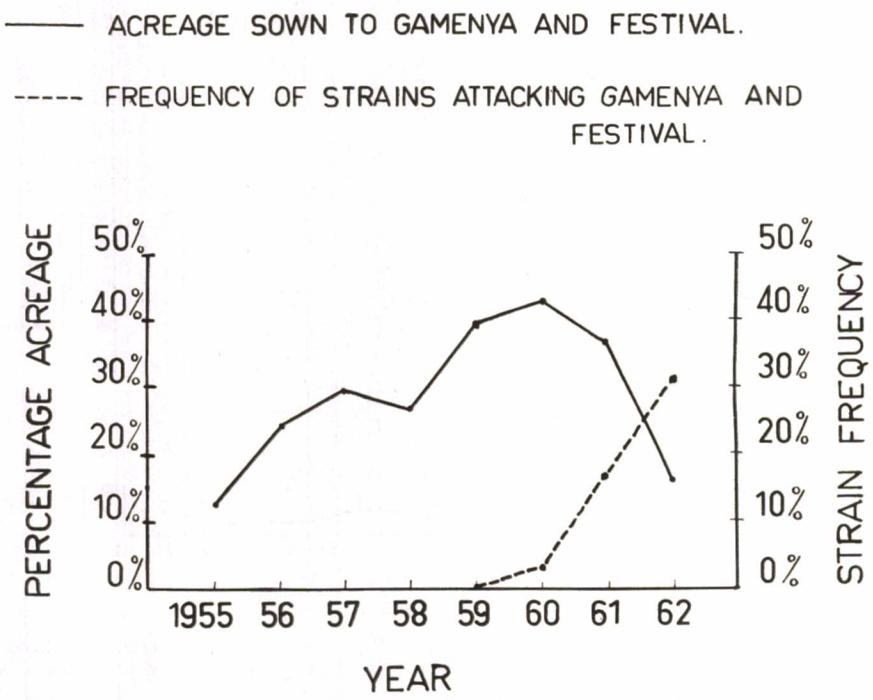

Fig. 3. The relationship between the percentage acreage sown to Gamenya and Festival in Queensland and the percentage frequency of strains attacking them found in Queensland and in northern New South Wales.

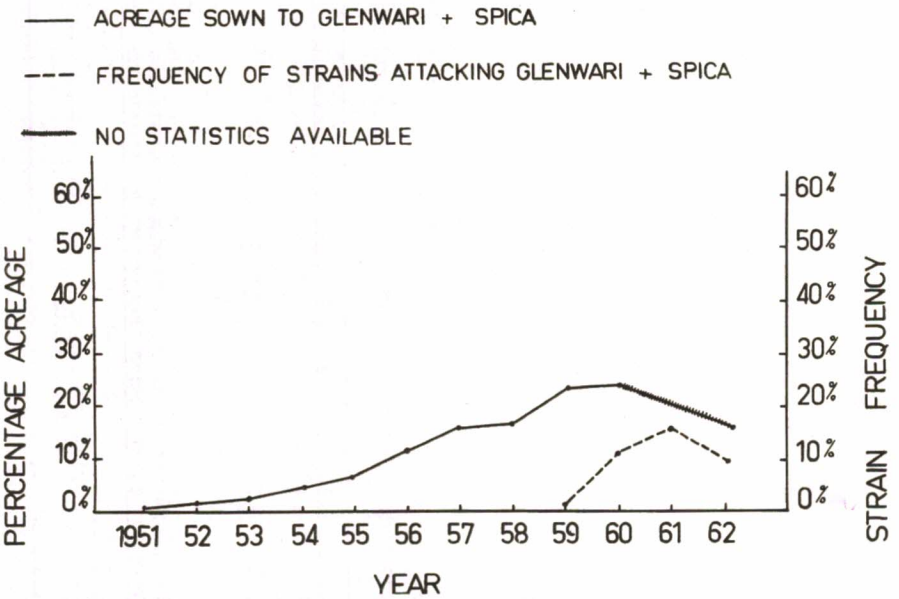

Fig. 4. The relationship between the percentage acreage sown to the varieties Glenwari and Spica in New South Wales and the frequency of rusts attacking them obtained from New South Wales and Queensland.

the marked discrepancy shown for 1955 has already been commented upon (Watson, 1958) and represents the rapid build up of strain 21–0 after its first appearance late in 1954 (1955 period). The decline in the acreage of varieties with Sr11 is clearly evident, but when statistics become available for 1961 and 1962 it is probable that Mengavi (Sr11) will have recovered much of the ground lost following the reduction in the acreage sown to Gabo.

Since no acreage figures are available for New South Wales for the last two seasons, those from Queensland have been used for Figures 3 and 5, although the rust figures have been a combined total for both areas. Gamenya has not proved popular in Queensland following only one year of trial when strain 21–2,3 was present, and this strain, too, has been responsible for the decline in the popularity of Festival. However, the upward trend of the rust frequency curve is due to the rapid expansion of the acreage sown to Gamenya in New South Wales, and consequently in the build up of the frequency of the strains attacking it.

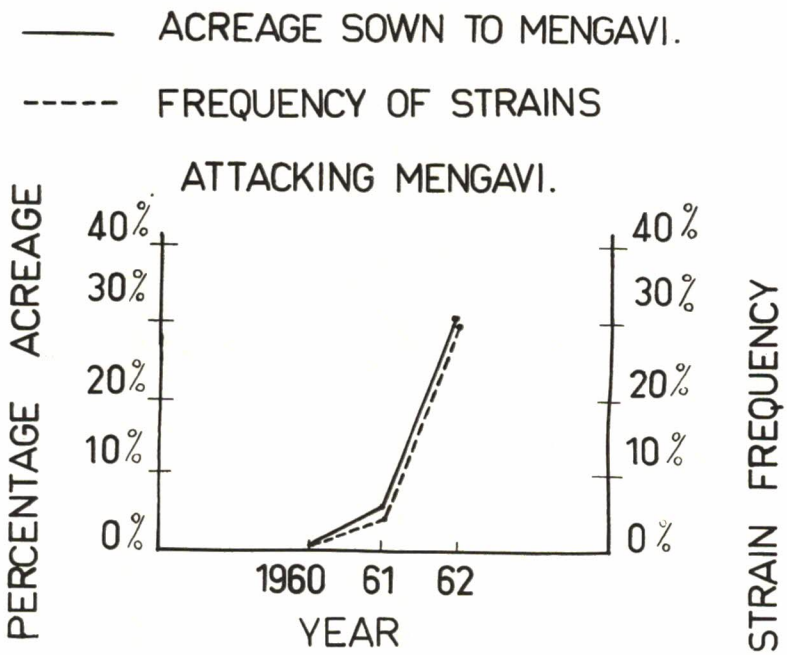

Fig. 5. The relationship between the percentage acreage sown to Mengavi in Queensland and the percentage recovery of strains attacking it in Queensland and northern New South Wales.

In Figure 4 the acreage sown to Glenwari and Spica in New South Wales as a whole increased steadily from 1951 to 1960, but an estimated decline has now occurred due to the release of Falcon and Heron in the south of the State to replace Glenwari, and of Mengavi and Gamenya in the north to replace Spica. The rusts have shown a downward trend in frequency in line with the estimated decline in acreage. Finally, the graphs of Figure 5, although for a period of only three years, show a very close agreement between the area of Mengavi cultivated and the intensity of the strain capable of attacking it.

Conclusions.

The varieties selected by Stakman and Levine for the separation of "standard" races of stem are still of considerable value for describing rust strains, but their limitations must be recognized. Among these varieties are genes for resistance that are as useful as any available for describing the pathogenicity of a particular collection of

rust. The genes of Kanred, Mindum, Vernal, Acme, Einkorn and Khapli are recognized throughout the world. However, they reveal only part of the complete phenotype of the rust and in each geographical area must be supplemented by genes contained in other varieties. Genes present in six such varieties have been described for the Australia–New Zealand area.

The system of classification used in this paper is simple, practical and self-explanatory and further differentials may be added from time to time as new genes become utilized by the wheat breeders. The resistance of Marquillo, Khapstein, *Agropyron* and probably of the unexplored varieties of *Triticum durum* doubtless will be utilized in Australian varieties of the future. In the meantime, however, those concerned in knowing the phenotype and possibly the genotype of various collections of rust in any area will need to utilize a system that is both convenient and effective. In addition to testing new genes, new combinations of old genes will need to be synthesized from time to time to facilitate the description of the rust strains. With the periodical changes of these latter, the most effective screening devices will vary with them.

A breeder may ignore the usefulness of strain separation and identification and concentrate on a resistance not controlled by major genes. However, evidence suggests that a single type of resistance is not enough and that the broad genetic base comprising several known genes is likely to be most valuable in giving a lasting protection. This broad base can only be built up and be effective against strains with known pathogenicity and this latter character can now be described with considerable accuracy.

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differently from one with Sr9 from Kenya 117A when these are tested with either Canadian or Australian strains of stem rust. It has been suggested therefore that the gene from Red Egyptian be designated Sr9a and that from Kenya 117A Sr9b. Under these circumstances the gene Kb_1 of Athwal and Watson (1954) is probably Sr9b.

Festival was released in 1950 and gained in popularity among farmers. For a few years no virulent strains of rust were found on it and there appeared a possibility that the gene Sr9 was affected less than other genes by changes in pathogenicity of the fungus. Hence, in 1958 Gamenya, also with Sr9 but with a more desirable quality and higher yield, was made available for commercial production (Watson *et al.*, 1960). The area sown to Festival in Queensland had increased to 43·2 per cent of the total during 1960–61, and from observations made by Mr. J. Bligh and from material he sent

TABLE 5.

Summary of the Number of Isolations of the various Strains grouped according to their Origin, in the Years 1952–1963.

Strain	State where Collected.								Total.
	N.S.W.	Q'ld.	Vic.	S.A.	W.A.	Tas.	A.C.T.	N.Z.	
17–Anz–2	4	1	—	—	—	—	—	—	5
17–Anz–1,2	3	—	—	—	—	—	—	—	3
21–Anz–0	421	27	65	31	—	29	—	29	602
21–Anz–2	1204	218	83	76	303	49	1	92	2026
21–Anz–5	184	79	2	1	—	8	—	28	302
21–Anz–1,2	73	5	1	4	66	—	—	—	149
21–Anz–2,3	273	118	1	—	—	1	—	6	399
21–Anz–2,5	6	—	1	—	—	—	—	—	7
21–Anz–2,6	3	—	—	—	—	1	—	—	4
21–Anz–1,2,3	86	18	—	—	—	—	—	1	105
34–Anz–0	—	—	—	—	—	—	—	7	7
34–Anz–2	397	23	10	16	—	7	—	6	459
34–Anz–4	1	1	—	—	—	1	—	—	3
34–Anz–1,2	10	—	—	—	—	—	—	—	10
34–Anz–2,4	219	113	—	—	—	—	—	—	332
34–Anz–2,5	3	—	—	—	—	—	—	—	3
40–Anz–2	2	—	—	—	—	—	—	—	2
116–Anz–2	—	2	—	—	—	—	—	—	2
116–Anz–2,3	19	8	—	—	—	—	—	—	27
126–Anz–6	156	17	41	11	151	11	2	7	396
126–Anz–1,6	24	3	10	—	15	7	—	2	61
126–Anz–2,6	73	9	2	7	—	3	—	—	94
222–Anz–6	14	—	2	1	49	—	—	—	66
222–Anz–2,6	137	33	12	4	—	—	1	—	187
222–Anz–1,2,6	57	8	3	—	—	1	1	—	70
222–Anz–1,2,4,6	1	—	—	—	—	—	—	—	1
Total ..	3370	683	233	151	584	118	5	178	5322

for examination it was clear that, as the gene Sr9 became exposed to rust over larger areas it offered no more lasting protection against rust than the two genes Sr6 and Sr11 used previously. The two strains attacking varieties with Sr9 have both been isolated first in Queensland, but each has moved south and both have now been found on Gamenya in New Zealand (Table 5).

Since the variety Kenya 117A W 1347, which was the source of the gene Sr9b, has other genes giving some resistance to the Australian rusts (Luig, 1961) the Marquis line W 2402 developed by Knott (Green *et al.*, 1960) is used in the survey work. Under field conditions to strains such as 21–2, W 2402 is much more susceptible than Kenya 117A and this is presumably on account of the broader genetic base of the latter which is concerned in rust resistance.

From the literature it appears that neither Sr9a nor Sr9b has been as useful as Sr6 and Sr11 in the subdivision of "standard" races. Green *et al.* (1960) have listed reaction types which show that either Sr9a or Sr9b or both are useful in separating

the components of "standard" races 11, 15, 29, 32 and 87, but little use appears to have been made of these genes in supplementals apart from what has been done in Australia.

4. *W 1656 (C.I.12632: (Ill. I × Chinese Spring)*^{2} *× T. timopheevi*; Allard & Shands, 1954*).—Triticum timopheevi* has been found to be highly resistant to stem rust in Australia as elsewhere and Allard and Shands (1954) transferred some of the resistance by backcrossing to derive the line C.I.12632. The latter is an attractive 42-chromosome parent which has resistance to many strains of stem rust and carries the Chinese type of adult plant resistance to leaf rust. It was used as the source of resistance to stem rust in the breeding of Mengavi (Watson *et al.*, 1960). In May, 1959, a year after the release of Mengavi, a single pustule was found on it at Brookstead, Queensland, by Mr. J. E. Bligh. From this the important strain 34–2,4 was isolated and, although it was not recovered from the field for another eighteen months, it built up at the end of 1961, oversummered in quantity and damaged Mengavi crops in Queensland in 1962–63. So far this strain is the only one in the field known to attack Mengavi.

The genetic system governing the resistance of *T. timopheevi* derivatives is not yet completely understood. Allard and Shands (1954), in the original work, found that in C.I.12633, a selection related to C.I.12632, the resistance to stem rust was controlled by duplicate dominant genes linked with a recombination value of 14·8 per cent, and Nyquist (1957) located these genes on chromosome XIII. Our studies, which are quite incomplete, show that when Federation is crossed with C.I.12632 and the progeny is tested with strain 126–1,6 the F_1 is resistant and the F_2 segregates in approximately a 3:1 ratio. However, when Eureka replaces Federation in the cross, both seedlings and adult F_1 plants are susceptible to strain 126–1,6 and the ratio in F_2 is different from that in which Federation is the susceptible parent. Pugsley (1959) has suggested that this type of result on F_1 plants may be a specific test for Sr6.

In more recent work Nyquist (1962) has found that when C.I.12633 is crossed with various susceptible varieties the percentage of susceptible plants in F_2 ranged from 26·6 to 7·1, and he proposed differential fertilization as a major cause of these variations. Regardless of whether one or more genes in C.I.12632 condition resistance to strains other than 34–2,4 it is quite clear that the complete resistance of the original species *T. timopheevi* has not been transferred. During 1962–63 when several hundred collections of rust on Mengavi were examined, all attacked C.I.12632, but from approximately 150 which were placed on seedlings of *T. timopheevi* not a single susceptible pustule was found on this species. Similar results have been found in North America where "standard" race 15 attacks C.I.12633 but not *T. timopheevi.* Certain strains, however, occur in the United States which are virulent on this species; in fact it can be used there as a supplemental to separate into components "standard" races 11, 15 and 29 (Stakman *et al.*, 1962).

Apart from the North American and Australian continents the resistance of C.I.12632 and C.I.12633 is also useful in Africa for subdividing "standard" races of stem rust. Guthrie (personal communication) reports that of six components of "standard" race 40 one is virulent on the above two derivatives of *T. timopheevi.*

5. *Renown W 2346 (H–44 × Reward).*—The adult plant type of resistance that has been used generally by wheat breeders originates from H–44 and Hope. The latter has been incorporated by Australian workers into the pedigree of Hofed, Warigo, Panther, Glenwari, Gala and Lawrence (Macindoe and Brown, 1958). For many years all were highly resistant to stem rust as adult plants but susceptible as seedlings to the prevalent strains. Seedling selections made in the glasshouse were of no use, but, during the years 1927 to 1941 at the Universities of Sydney and Adelaide, selection work in the field was aimed to get resistance to strain 126–6 which was by far the most prevalent at the time. The undertaking was highly successful, and from the Sydney programme Hofed was developed while Warigo, Glenwari and Panther were evolved at Adelaide (Macindoe and Brown, 1958).

The status of the seedling and adult plant reactions of Hope and Hope derivatives was drastically affected following the isolation of strain 21–0 in 1954. An additional