THE INHERITANCE OF RUST RESISTANCE.

IV. MONOSOMIC ANALYSIS OF RUST RESISTANCE AND SOME OTHER CHARACTERS IN SIX VARIETIES OF WHEAT INCLUDING GABO AND KENYA FARMER¹

D. R. KNOTT²

University of Saskatchewan, Saskatoon, Saskatchewan

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ABSTRACT

In previous papers in this series, 7 genes, designated *Sr6*–*Sr12*, controlling resistance to stem rust were identified. To determine the chromosomes carrying these genes, each of the 21 Chinese monosomics was crossed with the varieties, Gabo, Kenya Farmer, Egypt Na95 and Veadeiro. In addition mono-X was crossed with Lee and mono-XX with Red Egyptian. The F₂ populations from the crosses were tested with either or both of races 15B and 56 and in some cases were classified for other characters.

The gene *Sr7* was found to be on chromosome VIII but not linked to the gene *Hd* (Hooded). The locations of genes *Sr6*, *Sr8*, *Sr9*, *Sr11* and *Sr12* have been reported by other authors and were confirmed as follows: *Sr6*—chromosome XX, *Sr8*—chromosome VI, *Sr9*—chromosome XIII, *Sr11* and *Sr12*—chromosome X (28% recombination).

INTRODUCTION

The production by Sears (12, 14) of a complete series of monosomic and nullisomic lines in wheat has greatly facilitated linkage studies. Ordinary genetic methods are difficult to use in wheat because of its large number of chromosomes ($n = 21$) and its polyploid nature. By the use of the various aneuploids, chromosomes carrying specific genes can be identified.

Four methods of using the aneuploids to locate genes have been described by Sears (13). A procedure involving chromosome substitution has been used extensively by Sears, Loegering and Rodenhiser (15) and by Kuspira and Unrau (8, 9). In this procedure each of the 21 chromosomes of the variety under study is individually substituted for its homologue in a second variety. A number of backcrosses are made so that the second or recurrent parent is reconstituted except for the single substituted chromosome. The 21 substitution lines are then compared with both parents to determine the effect of each chromosome.

A procedure which involves less crossing and cytological study, and consequently requires less time and labour, is the study of F₂ populations from crosses between a variety and the 21 monosomics or nullisomics. The method works well for simply inherited dominant characters and has been used by several authors (4, 11, 16, 17) in studies on characters such as rust resistance. The location of a gene is determined by observing the segregations obtained in the F₂ populations derived from monosomic F₁ plants. With a single dominant gene a large excess of the dominant class over the expected 3:1 ratio will be obtained. A modification involving the study of F₁ plants has been used by Campbell and McGinnis (3).

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² Associate Professor of Field Husbandry, University of Saskatchewan, Saskatoon, Sask.

In previous papers of this series, Knott and Anderson (7) and Knott (5, 6) have identified and named a number of genes conditioning resistance to stem rust. The results of studies begun in 1952 to determine the chromosomes carrying these genes are reported in the present paper. Relatively complete studies were made on the varieties Gabo and Kenya Farmer and some additional work was done on Lee, Egypt Na95, Veadeiro and Red Egyptian. In all cases the F_2 method of monosomic analysis was used.

REVIEW OF LITERATURE

The monosomic analysis of Gabo was started before Knott and Anderson (7) discovered that the variety carries the same genes for resistance as Timstein and Lee. Sears and Rodenhiser (16) have shown that for resistance to race 56, Timstein has two dominant, complementary genes which are linked on chromosome X. Plessers (11) came to the same conclusion for Lee and obtained a recombination value of 29.5 per cent between the two genes. On the basis of comparative reactions to a number of races of leaf and stem rust, Watson and Stewart (18) concluded that Gabo, Timstein and Lee all derived their rust resistance from the durum variety, Gaza. Knott and Anderson (7) used the symbols *Sr11* and *Sr12* for the two complementary genes.

Knott (5, 6) reported that Kenya Farmer carries one gene, *Sr7*, for resistance to race 15B and four genes, *Sr9*, *Sr10*, *Sr11* and *Sr12*, for resistance to race 56. Aslam and Ausemus (2) have suggested that Kenya Farmer carries one gene for resistance to race 15B but in addition has the recessive alleles of two dominant, epistatic genes for susceptibility carried by Lee, Mida and Thatcher. The two recessives act as complementary genes conditioning a mesothetic (X) type of resistance. However, the results from crosses of Kenya Farmer with Egypt Na95 and Timstein-Henry are fitted to a single gene ratio.

Egypt Na95 was shown by Knott and Anderson (7) to have gene *Sr7* for resistance to race 15B and genes *Sr9* and *Sr10* for resistance to race 56. Aslam and Ausemus (2) reported that Egypt Na95 is susceptible to race 15B.

Knott (5) reported that Veadeiro carries genes *Sr9* and *Sr10* for resistance to race 56. In addition the variety has mature plant resistance to race 15B which may be conditioned by two genes.

MATERIALS AND METHODS

A brief description of the varieties used in this study is given below: *Gabo* (C.I. 12795)—An Australian variety from the cross Bobin² x Gaza. Gabo is resistant to race 56 but susceptible to race 15B.

Kenya Farmer (Kenya 338 AC. 2.E.2, P.I. 187165)—A Kenya variety from the cross (Button's x 73.D.21.1. (L)) x (Bobin² x Gaza). Kenya Farmer has good resistance to both race 15B and race 56.

Lee (C.I. 12488)—A Minnesota variety from the cross Hope x Timstein (sib of Gabo). Lee is similar to Gabo in rust reaction.

Egypt Na95 (C.I. 12894)—A Kenya variety from the cross Kenya U x 9 M.I.A.3. Egypt Na95 is resistant to races 15B and 56.

Red Egyptian (C.I. 12345)—An Ethiopian variety having good resistance to races 15B and 56.

Veadeiro (P.I. 192475)—A Portuguese variety. Veadeiro is resistant to race 56 and has mature plant resistance to race 15B.

Gabo, Kenya Farmer, Veadeiro and Egypt Na95 were each crossed with the 21 Chinese monosomics and with normal Chinese. Lee was crossed with only a few of the monosomics. In some cases the most vigorous nullisomics (I, VII, XI, XIV and XXI) were used either in addition to or in place of the corresponding monosomic. Rust tests were conducted on the F₂ populations and in some cases on F₃ families. The methods of conducting seedling and field rust tests have been reported in previous papers in this series.

Aceto-carminc smears were used for cytological studies of meiosis in pollen mother cells.

RESULTS

GABO AND LEE

Rust Resistance

The F₁ plants from the crosses between the aneuploids and Gabo were not studied cytologically. It was hoped that by growing a sufficiently large number of F₂ families from each cross, the critical monosomic line or lines could be determined on the basis of a disturbed F₂ ratio. (The critical line is the one which is monosomic for the chromosome carrying the gene under study).

Large F₂ populations from the Gabo crosses were grown in the field in 1953 under an artificial epidemic of race 56. No natural rust infection developed in the Saskatoon area and, consequently, only race 56 was present in the nursery. Gabo was found to carry as high as 30 per cent of moderately resistant type pustules. Typically the stem pustules were small, round, and partially covered by a flap of epidermis. Since even the resistant parent showed considerable rust, the separation of resistant and susceptible plants in F₂ populations was difficult. Furthermore, the F₂ progeny segregated for lateness and winter habit and this also complicated classification. Only those plants that had headed by the end of the growing season were classified for rust reaction.

TABLE 1.—SEGREGATION FOR RESISTANCE TO RACE 56 IN F₂ SEEDLINGS FROM THE CROSSES, CHINESE X GABO AND MONO-X X GABO

Female parent	F ₁ plants	Number of F ₂ plants	
		Resistant	Susceptible
Chinese	Normal	99	53
Mono-X	Normal	28	17
	Mono-X	172	3

The segregation in the cross between normal Chinese and Gabo was a good fit to a ratio of 1 moderately resistant : 15 susceptible plants (actual segregation 69:976). This seemed to indicate that two complementary recessive genes conditioned resistance. Since the genes were recessive, a disturbance of the F_2 ratio in the critical monosomic line or lines would depend on the genes being effective when hemizygous. Actually, none of the F_2 populations had significantly more than 1 resistant plant in 16 and many had less. Consequently, the chromosome or chromosomes carrying the genes could not be determined.

In the same summer that the field tests were made, Knott and Anderson (7) found that a cross between Gabo and Timstein did not segregate for resistance to race 56. On the basis of this and other data they concluded that Gabo and Timstein are sibs from the same cross. A similar conclusion was reached by Watson and Stewart (18). Since Sears and Rodenhiser (16) have shown that seedling resistance in Timstein is conditioned by two dominant complementary genes on chromosome X, it was assumed that the same two genes were present in Gabo. The F_2 seedlings from crosses between Chinese and Gabo, and monosomic X and Gabo were, therefore, tested with race 56. The results are given in Table 1. Gabo shows a type 1⁺ reaction to race 56 and in the F_2 populations a clear segregation for type 1⁺ and type 4 reactions was obtained. The segregation in the cross with normal Chinese is close to a 9:7 ratio but an excess of resistant plants is present, indicating that resistance is controlled by two dominant, complementary, linked genes. Almost all of the F_2 progeny of mono-X F_1 plants were resistant showing that both genes are carried on chromosome X. There is little doubt that these same two genes condition field reaction to race 56 but apparently in the adult plant they behave as recessives and are not effective in the hemizygous condition. Knott and Anderson (7) used the symbols *Sr11* and *Sr12* for them.

TABLE 2.—SEGREGATION FOR RESISTANCE TO RACE 56 IN F_2 SEEDLINGS FROM THE CROSSES, CHINESE $\times$ LEE AND MONO-X $\times$ LEE

Female parent	F_1 plants	Number of F_2 plants	
		Resistant	Susceptible
Chinese	Normal	372	229
Mono-X	Normal	113	62
	Mono-X	87	0

TABLE 3.—RECOMBINATION BETWEEN *Sr11* AND *Sr12* CALCULATED FROM THE F_2 DATA

Cross	Number of F_2 plants		Recombination value (%)
	Resistant	Susceptible	
Chinese $\times$ Gabo F_2	127	70	24 $\pm$ 9.0
Chinese $\times$ Lee F_2	485	291	29 $\pm$ 4.9

Pooled value = 28 $\pm$ 4.3
Heterogeneity χ^2 = .2606

As a check on the F_2 results further studies were made on F_3 lines from the mono-X $\times$ Gabo cross. Nineteen F_3 lines derived from mono-X F_1 plants were grown. In seedling tests 449 plants in these lines were resistant and 11 susceptible, confirming the F_2 results.

Since the variety, Lee, is a hybrid involving Timstein, it should also carry the genes, *Sr11* and *Sr12*, on chromosome X. The F_2 seedlings from a cross between mono-X and Lee were tested with race 56. The results are given in Table 2. As expected the data show that Lee carries two genes on chromosome X and, thus, agree with the results obtained by Plessers (11).

Sears *et al.* (15) have shown that Hope, which is one of the parents of Lee, has a gene for rust resistance on chromosome VIII. The F_2 seedlings from a cross between mono-VIII and Lee were tested with race 56 but no evidence was obtained that this chromosome carried a gene for rust resistance.

The F_2 data from the crosses between Chinese and Gabo, and Chinese and Lee were used to obtain a measure of the recombination between *Sr11* and *Sr12*. The results are given in Table 3. It appears that *Sr11* and *Sr12* are about 28 crossover units apart. Plessers obtained a similar value, 29.5.

Growth Habit

The progeny from the cross between Gabo and Chinese segregated for winter growth habit. Classification of the F_2 families was somewhat difficult since a full range of types, including many very late plants, was present. When only those plants which failed to head by the end of the

TABLE 4.—SEGREGATION FOR WINTER HABIT IN F_2 POPULATIONS FROM CROSSES BETWEEN THE CHINESE MONOSOMICS AND GABO

Female parent	Number of F_2 plants		Ratio	P for a 1:63 ratio
	Winter habit	Spring habit		
Chinese	26	1045	1:40.2	.02-.05
Mono-I	7	406	1:58.0	1.0
-II	17	833	1:49.0	.30-.50
-III	20	878	1:43.9	.10-.20
-IV	13	909	1:69.9	.50-.95
-V	18	748	1:41.6	.10-.20
-VI	12	721	1:60.1	1.0
-VII	21	782	1:37.2	.02-.05
-VIII	18	892	1:49.6	.30-.50
-IX	31	947	1:30.5	<.001
-X	6	254	1:42.3	.30-.50
-XI	22	955	1:43.4	.10-.20
-XII	18	841	1:46.7	.20-.30
-XIII	14	803	1:57.4	.50-.95
-XIV	3	411	1:137.0	.20-.30
-XV	7	347	1:49.6	.50-.95
-XVI	2	170	1:85.0	.50-.95
-XVII	12	933	1:77.8	.50-.95
-XVIII	17	870	1:51.2	.30-.50
-XIX	10	654	1:65.4	1.0
-XX	9	570	1:63.3	1.0
-XXI	12	707	1:58.9	.50-.95

growing season were counted as winter types, the segregation approximated 1 winter : 63 spring. The data are given in Table 4. The cross with normal Chinese had a slight excess of winter plants with a P value of between .02 and .05 for a 1:63 ratio. All except 2 of the 21 monosomic crosses gave good fits to a 1:63 ratio. The cross involving mono-VII showed a small excess of winter plants and the cross with mono-IX a very large excess. There is little doubt, therefore, that Gabo has a gene for winter habit on chromosome IX. Sears (14) and Unrau (17) have reported that Chinese has a gene for spring habit on this chromosome.

If the 1:63 ratio is correct, then three complementary recessive genes are necessary to produce the full winter habit of growth. One variety must carry two of the genes and the other variety, one. As already indicated one of the genes is on chromosome IX of Gabo. If Gabo carries another gene for winter habit, then a second cross should have shown a substantial excess of winter plants. While this did not occur, in the cross between mono-XVIII and Gabo there was a large number of very late plants. This might mean that Gabo carries a gene for winter habit on chromosome XVIII but the gene is ineffective when hemizygous. Thus plants that were hemizygous for this gene and homozygous recessive for the remaining two genes would be late but not winter habit. Sears (14) has suggested that chromosome XVIII in Chinese carries a gene for spring habit since monosomic plants are late in heading. Thus Gabo could have an allele of this gene which conditions winter habit but it also could be that the many late plants in the cross between monosomic XVIII and Gabo are merely due to the absence of the gene for spring habit.

At least one of the genes for winter habit must be carried by Chinese. The F_1 plants that are monosomic for the chromosome carrying this gene should give F_2 progeny that are all spring habit. The cross with mono-XIV came closest to this, having only 3 winter habit plants out of 414. Since no cytology was done on the F_1 plants, all of the segregations obtained probably combine results from progeny of both monosomic and disomic plants and the 3 winter habit plants could have come from disomic parents. It is possible, therefore, that the winter habit gene in Chinese is on chromosome XIV. While the data are not too conclusive they suggest that Gabo has genes for winter habit on chromosomes IX and XVIII and Chinese has a gene on chromosome XIV.

Awns

Although Gabo is awnletted and Chinese is hooded the F_2 progeny from the cross segregated for awns. The F_2 families grown in the field were classified for awning but the segregations did not appear to fit any ratio. However, the cross with mono-IX contained fewer awned plants than the cross with normal Chinese and the crosses involving chromosomes VIII, XVI, XXI and possibly VII had more. The results agree fairly well with reports by Sears (14) who indicated that chromosome IX of Chinese carries the gene b_1 for non-inhibition of awns, chromosome VIII carries the gene Hd for hooded and chromosome XVI carries an inhibitor of awns. Sears did not report that chromosome XXI had any effect on awning; however, Heyne and Livers (4) found that it had an effect in the variety Pawnee.

KENYA FARMER

Rust Resistance

The F_1 plants from crosses between the Chinese monosomics and Kenya Farmer were studied cytologically. Even disomic plants showed a considerable number of micronuclei in pollen quartets. Metaphase counts showed that one chromosome pair failed to form a bivalent about 25 per cent of the time. No chain or ring of four was noted so that failure to pair must have been due to some cause other than a translocation. Pollen mother cells from monosomic plants frequently showed a configuration of $19_{II} + 3_I$ at metaphase instead of $20_{II} + 1_I$. The monosomic plants showed some sterility, particularly in the greenhouse, with certain crosses being much more sterile than others.

TABLE 5.—SEGREGATION FOR RESISTANCE TO RACE 15B IN F_2 SEEDLINGS FROM CROSSES BETWEEN THE CHINESE MONOSOMICS AND KENYA FARMER

Female parent	F_1 plants	Number of F_2 plants		P for a 3:1 ratio
		Resistant	Susceptible	
Chinese	Normal	33	7	.20-.30
Mono-I	Normal	13	6	.50-.95
	Mono-I	11	6	.30-.50
Mono-II	Normal	13	6	.50-.95
	Mono-II	51	7	.02-.05
Mono-III	Normal	18	2	.10-.20
	Mono-III	53	22	.30-.50
Mono-IV	Normal	13	6	.50-.95
	Mono-IV	27	12	.30-.50
Mono-V	Normal	16	6	1.0
	Mono-V	77	20	.30-.50
Mono-VI	Normal	16	4	.50-.95
	Mono-VI	62	16	.30-.50
Mono-VII	Mono-VII	30	9	.50-.95
Mono-VIII	Normal	29	10	1.0
	Mono-VIII	160	0	< .001
Mono-IX	Normal	18	5	.50-.95
	Mono-IX	58	20	1.0
Mono-X	Normal	16	4	.50-.95
	Mono-X	61	19	.50-.95
Mono-XI	Normal	14	6	.50-.95
	Mono-XI	40	15	.50-.95
Mono-XII	Normal	13	7	.30-.50
	Mono-XII	29	10	1.0
Mono-XIII	Normal	26	10	.50-.95
	Mono-XIII	25	12	.20-.30
Mono-XIV	Normal	15	5	1.0
	Mono-XIV	77	35	.10-.20
Mono-XV	Mono-XV	47	11	.20-.30
Mono-XVI	Normal	13	6	.50-.95
	Mono-XVI	29	9	1.0
Mono-XVII	Normal	15	5	1.0
	Mono-XVII	13	6	.50-.95
Mono-XVIII	Mono-XVIII	13	7	.30-.50
Mono-XIX	Normal	12	7	.20-.30
	Mono-XIX	64	16	.30-.50
Mono-XX	Normal	16	4	.50-.95
	Mono-XX	22	13	.05-.10
Mono-XXI	Mono-XXI	25	14	.10-.20

The F_2 progenies from both monosomic and disomic plants were grown in the field in 1954 under an epidemic of race 15B. While artificial inoculations were made only with race 15B, a heavy natural epidemic, which may have included other races, developed in the area. The epidemic was, however, very largely race 15B.

All of the F_2 plants were pulled and classified according to the percentage of rust on the stems. Kenya Farmer showed only a trace of rust whereas Chinese was highly susceptible. The F_2 plants from the Chinese $\times$ Kenya Farmer cross ranged from a trace to 60 per cent rust with 40 per cent of the plants having only a trace. The F_2 progeny from each of the crosses with the 21 monosomics ranged from a trace to at least 50 per cent rust. Although there was considerable variability among the crosses most of them contained about 40 per cent of plants showing only a trace of rust. The progeny of disomic F_1 plants showed as much variability as the progeny of monosomics and, as a result, the chromosome carrying the gene for resistance to race 15B could not be determined from the data.

In the same summer that the plants from the monosomic crosses were grown in the field, a number of families from a backcross of Kenya Farmer to Thatcher were tested in the field. As reported by Knott (5) the data from the backcrosses showed that Kenya Farmer carries one main gene for resistance to race 15B. The results indicated that the gene was only partially dominant so that heterozygotes carried up to 30 per cent rust. If hemizygotes react in a similar fashion to heterozygotes, in the critical monosomic cross only nullisomic plants and plants carrying an isochromosome or a telocentric chromosome lacking the gene for resistance should carry over 30 per cent rust. In the Chinese $\times$ Kenya Farmer cross 24.7 per cent of the plants had 30 per cent or more rust. In the monosomic crosses the only outstanding deviation from this percentage was for chromosome VIII where only 2 of 37 plants had more than 20 per cent rust. Unfortunately, F_1 plants monosomic for chromosome VIII had been largely sterile and, consequently, the number of F_2 plants tested was small and the significance of the deviation was considered doubtful.

The F_2 progenies from both monosomic and disomic parents were next tested in the seedling stage with both race 15B and race 56. The results are given in Table 5. With race 15B Kenya Farmer gave a 0; -1- type of reaction with considerable chlorosis and tip killing. In the F_2 progenies it was found that segregations fitting a ratio of 3 resistant : 1 susceptible plants were obtained if all plants having considerable chlorosis were called resistant. This meant counting as resistant some plants having an X+ reaction. The segregation in all but two of the F_2 progenies from both normal and monosomic F_1 plants, fitted a 3:1 ratio. The F_2 progeny of plants monosomic for chromosome II segregated 51 resistant : 7 susceptible with P for a 3:1 ratio falling between .02 and .05. Since 39 segregations were tested it is not surprising that one gave a P value below .05 and it is considered unlikely that the deviation is significant. From the cross with chromosome VIII, 160 F_2 plants were tested and all proved to be resistant. The results show clearly that the gene for resistance to race 15B carried by Kenya Farmer is on chromosome VIII. Knott (5) has shown that the gene is *Sr7*.

Since it has been suggested by Knott (5) that Kenya Farmer carries one major gene which modifies the resistance conditioned by *Sr7*, the data were studied for any indication of its location. The critical monosomic line should have all highly resistant and no moderately resistant plants if the modifier is effective when hemizygous. Neither the field nor the seedling tests showed any cross having such a deviation from the normal.

The results from tests with race 56 on F_2 populations from crosses between the monosomics and Kenya Farmer were more difficult to analyse. Knott (5, 6) has shown that for resistance to race 56, Kenya Farmer has two, dominant, independent genes, *Sr9* and *Sr10*, plus two dominant, complementary genes, *Sr11* and *Sr12*, the latter being on chromosome X. With 28 per cent crossing over between *Sr11* and *Sr12* the expected F_2 ratio is approximately 42 resistant to 1 susceptible plant. With such a ratio it is almost impossible to determine the critical chromosome lines by an F_2 analysis. A few susceptible plants will be present even in the critical monosomic lines due to the presence of nullisomic plants and plants which, as a result of misdivision of the univalent, have lost the chromosome arm carrying the gene for resistance.

Small F_2 populations were tested with race 56 and the results gave no indication of the location of the genes for resistance. In general more susceptible plants than expected were obtained, probably due to the fact that *Sr10* is only partially dominant and heterozygotes are difficult to distinguish from fully susceptible plants. Further tests were made on F_3 lines. Theoretically, if no misdivisions occur it should not be possible to get a homozygous susceptible F_3 line from one of the critical crosses, except as the progeny of a nullisomic. A nullisomic line would be readily detectable morphologically. A test was, therefore, made on the F_3 progeny of susceptible F_2 plants from each of the 21 monosomic crosses except VIII and XIII in which no susceptible plants had been obtained. For chromosomes VIII and XIII, F_3 lines from F_2 plants which had not been tested with race 56 were grown. Homozygous susceptible F_3 lines were obtained in all crosses except those with monosomics XIII, XVI and XVII. Additional tests with race 56 were made on F_2 populations from these three crosses and the results are given in Table 6. The data show clearly that one of the genes conditioning resistance to race 56 is on chromosome XIII. Sears, Loegering and Rodenhiser (15) have reported that Red Egyptian carries gene *Sr9* on chromosome XIII. The results are, therefore, in agreement.

TABLE 6.—SEGREGATION FOR RESISTANCE TO RACE 56 IN F_2 SEEDLINGS FROM CROSSES BETWEEN MONOSOMICS XIII, XVI AND XVII AND KENYA FARMER

F ₁ parent	Number of F ₂ plants	
	Resistant	Susceptible
Mono-XIII	229	0
Mono-XVI	244	5
Mono-XVII	213	7

TABLE 7.—SEGREGATION OF THE GENES *Sr7* AND *Hd* ON CHROMOSOME VIII

Cross	Number of families			
	Homozygous <i>Hd</i>		Segregating <i>Hd</i>	
	Seg. resistant	Susceptible	Seg. resistant	Susceptible
(K. Farmer × Chinese) × (Chinese) F ₂	16	11	17	13
	P for 1:1:1:1 ratio = .50-.95 28 parental, 29 non-parental combinations			
(K. Farmer × Chinese) × (Marquis) F ₂	Segregating <i>Hd</i>		Homozygous <i>hd</i>	
	Seg. resistant	Susceptible	Seg. resistant	Susceptible
	18	15	11	8
	P for 1:1:1:1 ratio = .20-.30 26 parental, 26 non-parental combinations			

The location of the second and weaker gene, *Sr10*, is still in doubt. The gene is now being transferred alone to Marquis by backcrossing and a homozygous line will be crossed with the monosomics.

In the initial tests with race 56 no indication of a gene or genes on chromosome X was obtained. However, since other work by Knott (6) had shown that Kenya Farmer carries *Sr11* and *Sr12*, a second sample of F₂ seedlings from the cross, monosomic X × Kenya Farmer was tested with race 56. Of 95 plants from monosomic F₁ parents, 94 were resistant and 1 susceptible. The resistant plants all gave the type 1+ or better reaction that is typical of *Sr11* and *Sr12* and it seems evident that Kenya Farmer does carry the two genes.

Test for Linkage between Sr7 and Hd

Since *Sr7* was found to be on chromosome VIII and Sears (14) has reported that the gene for hoods, *Hd*, is also on chromosome VIII, a test for linkage was made. The F₁ plants from a cross between Kenya Farmer and Chinese were backcrossed to the hooded parent, Chinese, and were also crossed to Marquis, which carries the recessive alleles of both genes. One hundred and nine F₂ families were tested twice, first in the field under an artificial epidemic of race 15B and second, in the greenhouse using seedling tests with race 15B. The results of the two rust tests were in complete agreement and fitted a ratio of 1 segregating : 1 susceptible family. Unfortunately in both the cross with Marquis and the backcross to Chinese, some difficulty was experienced in the classification for the hooded character. In the backcross, the difference between a homozygous hooded and a segregating family was reasonably clearcut and the results are considered to be reliable. They are given in the top part of Table 7 and show no indication of linkage. In the cross to Marquis the separation of families segre-

gating for hooded from those homozygous for non-hooded was extremely difficult, partly due to the occurrence of many awnless plants. The results from the field test gave a reasonable fit to the expected 1:1 ratio and the results are given in the lower part of Table 7. There was no evidence of linkage and it is concluded, therefore, that although *Sr7* and *Hd* are both on chromosome VIII, they assort independently of one another.

EGYPT Na95

Considerably more sterility was present in the crosses involving Egypt Na95 than in those from other parents. The 21 F_2 populations from crosses with the monosomics were tested in the field with race 15B and in the seedling stage with races 15B and 56. None of the results was particularly good, although there was some indication that resistance to race 15B was due to a gene on chromosome VIII. When it was found by Knott and Anderson (7) that the genes for resistance carried by Egypt Na95 were also present in Kenya Farmer, work on the variety was dropped.

RED EGYPTIAN

Knott and Anderson (7) have shown that Red Egyptian carries three genes for resistance to races 15B and 56 of stem rust. The gene *Sr6* conditions a high resistance to both races, *Sr8* conditions moderate resistance to both and *Sr9* conditions moderate resistance to race 56. Peterson and Campbell (cited by Sears—14), and Sears *et al.* (15) have shown that *Sr6* is on chromosome XX. Sears *et al.* have also indicated that *Sr8* is on chromosome VI and *Sr9* on chromosome XIII.

Since Knott and Anderson (7) found that *Sr6* is dominant with race 56 but recessive with race 15B, plants from the cross, Chinese monosomic XX $\times$ Red Egyptian, were tested with both races to see how the gene behaved when hemizygous. The monosomic F_1 plants gave a fleck reaction to both races so *Sr6* must be effective against both when hemizygous.

Anderson (1) noted a linkage between *Sr6* and the gene *C* for compact spike. To measure this linkage, Red Egyptian was crossed and backcrossed to Marquis and the F_1 plants were tested with race 56 and classified for head type. The number of plants of each genotype was as follows:

<i>Sr6 C</i>	<i>Sr6 c</i>	<i>sr6 C</i>	<i>sr6 c</i>
96	25	19	103

The percentage of recombination is 18.1.

VEADEIRO

Veadeiro has been shown by Knott (5) to carry two genes *Sr9* and *Sr10*, conditioning resistance to race 56. In addition, it has mature plant resistance to race 15B.

In an attempt to locate the factor or factors for mature plant resistance, F_2 families from the 21 crosses between the Chinese monosomics and Veadeiro were tested in the field under an epidemic of race 15B. The plants were classified according to the percentage rust on the stems. All of the families appeared to show the same range of segregation and no indication of the chromosome(s) involved in resistance was obtained.

TABLE 8.—CHROMOSOME LOCATIONS OF SOME GENES FOR STEM RUST RESISTANCE.

Gene	Chromosome	Variety	Authority
<i>Sr6</i>	XX	McMurachy	Peterson and Campbell (cited by Sears—14)
		Red Egyptian	Sears <i>et al.</i> (15) Knott (this paper)
<i>Sr7</i>	VIII	Kenya Farmer Egypt Na95 Kenya Governor	Knott
<i>Sr8</i>	VI	Red Egyptian	Sears <i>et al.</i> (15)
<i>Sr9</i>	XIII	Red Egyptian Kenya Farmer Veadeiro	Sears <i>et al.</i> (15) Knott
<i>Sr10</i>	Unknown		
<i>Sr11</i> and <i>Sr12</i>	X	Timstein	Sears and Rodenhiser (16) Sears <i>et al.</i> (15)
		Gabo	Knott
		Lee	Plessers (11) Knott

Veadeiro has two genes, *Sr9* and *Sr10*, in common with Kenya Farmer. Since results with the latter variety had indicated that chromosomes XIII, XVI and XVII might be involved, F₂ populations from the crosses of Veadeiro with the three monosomics were tested with race 56. In the cross with monosomic XIII only 2 of 169 plants were susceptible, confirming that one gene is on chromosome XIII. The segregations in the other two populations fitted the expected 15:1 ratios.

DISCUSSION

The results reported in this paper, in conjunction with those of other authors, have made it possible to identify the chromosomes carrying all of the genes from *Sr6* — *Sr12* with the exception of *Sr10*. A list of the genes, their chromosome location, the varieties in which they have been located and the authority is given in Table 8.

It is gratifying to find that the results in this paper and in earlier papers in the series agree so completely with those of Sears, Loegering and Rodenhiser (15). The best example is the variety Red Egyptian. From the study of backcrosses to a susceptible variety Knott and Anderson (7) showed that Red Egyptian has one gene, *Sr8*, which conditions moderate resistance to both races 15B and 56, a second gene *Sr9*, which conditions moderate resistance to race 56 and a third gene, *Sr6*, which conditions high resistance to both races. Sears, Loegering and Rodenhiser (15) substituted each of the Red Egyptian chromosomes singly into Chinese and obtained three lines which were rust resistant. The chromosome VI substitution line was moderately resistant to races 15B and 56, the chromosome XIII line was moderately resistant to race 56 and the chromosome XX line was

highly resistant to race 56. The latter line was listed as susceptible to race 15B but Loegering and Geis (10) have shown that at lower temperatures it is also highly resistant to this race. Thus the correspondence is complete. Knott (5) has reported that gene *Sr9* is common to Red Egyptian, Kenya Farmer and Veadeiro. By the F_2 method of monosomic analysis it has been shown that Kenya Farmer and Veadeiro have a gene on chromosome XIII. This again agrees with Sears' results on Red Egyptian.

The results reported in this paper and in papers by Knott and Anderson (7) and Knott (5, 6) show some disagreement with those obtained by Aslam and Ausemus (2) for the varieties Kenya Farmer, Kenya 117A and Egypt Na95. However, most of the discrepancies can easily be accounted for. With Kenya 117A, stocks having different C.I. numbers were used. Watson and Stewart (18) have shown that there are two supposed Kenya 117A's in use and that they differ greatly in rust reaction. The author did some work with the Minnesota line (C.I. 12568) and found that it has the same genes for rust resistance as does Kenya 58. Aslam and Ausemus obtained similar results from the crosses of Kenya 117A and Kenya 58 with Kenya Farmer as would, therefore, be expected.

Egypt Na95 has generally been reported to be resistant to race 15B. Knott and Anderson (7) noted that the variety was not homogeneous so it is not surprising that Aslam and Ausemus obtained a susceptible stock.

The discrepancies with regard to Kenya Farmer are more difficult to explain. Fortunately, however, there is agreement that the variety carries one main gene for resistance to race 15B. According to the genotypes suggested for Kenya 58 and Kenya 117A by Knott and Anderson (7) the crosses of these two varieties with Kenya Farmer should not segregate for resistance to race 15B. In both crosses Aslam and Ausemus (2) found 1 F_3 line in 64 to be susceptible.

As reported by Knott and Anderson (7) and by Knott (5, 6) the gene *Sr7* is particularly subject to the action of modifying genes, with the genes *Sr9* and *Sr10* apparently being two of the more important ones. The author has found in transferring *Sr7* to the susceptible variety Marquis, that only a very moderate type of resistance is recovered. A homozygous line, obtained after five backcrosses, typically gives a type 3 reaction with considerable chlorosis. In the crosses of Kenya Farmer with Kenya 58 and Kenya 117A, gene *Sr7* would be homozygous but *Sr6*, *Sr9* and *Sr10* would be segregating. Thus 1 F_3 line in 64 would be homozygous for *Sr7* but lack all three of the remaining genes. Such a line might well have given a type 3c (chlorotic) reaction and been classified as susceptible according to the system used by Aslam and Ausemus.

During the course of this study it became evident that field rust tests are of little use in monosomic studies. From four complete sets of monosomic crosses tested in the field, no useful data were obtained. Apparently, so many uncontrolled factors affect field reactions that the readings are unreliable.

In using the F_2 method of monosomic analysis, it appears desirable to study the F_1 plants cytologically and to grow F_2 progenies from both monosomic and normal sibs. Comparing the progenies of sibs is more satisfactory than comparing the progeny of a monosomic with the progeny from a cross with normal Chinese.

A big problem, particularly in the crosses with Egypt Na95, was sterility. Monosomic plants are usually more sterile than their normal sibs and the bagging of heads on F_1 plants is essential.

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