GENETIC AND CYTOGENETIC STUDIES OF STEM RUST, LEAF RUST, AND POWDERY MILDEW RESISTANCES IN HOPE AND RELATED WHEAT CULTIVARS

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Summary

Three linked genes responsible for resistance respectively to stem rust, to leaf rust, and to powdery mildew are located on chromosome 7B of Hope wheat. The gene for stem rust resistance, operative in seedling and adult plant stages, is recessive and is designated *sr17*. The incompletely dominant gene for resistance to leaf rust, designated *Lr14*, showed 18% recombination with *sr17*, whilst in two different crosses recombination estimates of 6·0 and 2·5%, respectively, were obtained for the recessive gene for mildew resistance and *sr17*. All three genes were found to be present in a high proportion of Hope and H-44 derivatives. The gene *sr17* is apparently ineffective in conferring resistance to North American and pre-1954 Australian stem rust strains. Its incorporation into several cultivars selected for resistance to these strains presumably resulted from gene interactions or linkage with genes for resistance to other diseases.

I. Introduction

The cultivars Hope and H-44 of hexaploid bread wheat (*Triticum aestivum* L. emend. Thell. subsp. *vulgare* MacKey) possess high resistance to certain strains of stem rust (*Puccinia graminis* var. *tritici* Eriks. & Henn.) transferred from the tetraploid wheat, Yaroslav Emmer (*T. dicoccum* Schübl.) (McFadden 1930). Although they were agronomically unsatisfactory, their resistances were subsequently incorporated into many commercially adapted cultivars, both American and Australian. Pan (1940) showed that the major factor for field resistance in Hope was identical with that in H-44. With the advent of stem rust race 15B in North America the resistance of these cultivars became ineffective. More recently in Australia certain derivatives of Hope and H-44 became susceptible to Spica-attacking strains, although Hope and H-44 still showed a certain degree of resistance. Watson and Luig (1961, 1963) reported that Spica, despite its alleged parentage, resembled Hope derivatives in field reaction to stem rust and seedling reaction to leaf rust, but that it did not appear to be susceptible to the head blackening expressed by many of those cultivars.

Hope, H-44, and many of their derivatives have been shown by several investigators to possess resistance to certain strains of wheat leaf rust (*Puccinia recondita* Rob. ex Desm.) and wheat powdery mildew (*Erysiphe graminis* DC. var. *tritici* Marchal). In the present studies it was found that many of the derivatives of Hope and H-44 possessed resistance to all three pathogens. This indicated that the resistances were probably genetically linked since a number of these cultivars were selected under field conditions and probably in the absence of selective leaf rust and mildew strains. For example, the cultivar Mendos was selected only for resistance

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to stem rust, but it also possesses Hope-type leaf rust and mildew resistances. This paper describes the reactions of Hope, H-44, and their derivatives to Australian strains of the pathogens and presents evidence of linkage between the host genes responsible for resistance to the three parasites.

Earlier results relating to the inheritance of stem rust resistance in Hope and H-44 by North American workers have been reviewed by Ausemus (1934, 1943). In instances where seedling and mature plant resistances were studied they were independently inherited and, in the majority of instances, determined by one or two factors. Neatby (1931) found that the mode of inheritance depended upon the particular rust strain used.

In Australian studies Churchward (1938) found that Hope possessed a single factor for seedling resistance which was independent of at least two factors for mature plant resistance to stem rust. Phipps, Hockley, and Pugsley (1943) reported that Warigo possessed adult plant but not seedling resistance to stem rust. In addition they noted Warigo's resistance to leaf rust and mildew.

By means of nullisomic analysis Longwell and Shirky (1952) located a gene for seedling stem rust resistance on chromosome 4B(VIII) of Hope. Sears, Loegering, and Rodenhiser (1957) found two chromosomes, 4B and 1D(XVII), involved in the seedling resistance of Hope against two different races respectively; however, they could associate no single chromosome with mature plant resistance. Using a monosomic series of Redman (a derivative of H-44), Campbell and McGinnis (1957) associated three chromosomes, 3B(III), 4B, and 2B(XIII), with seedling resistance to race 56 of stem rust. Recently the gene on Hope 4B was found to be allelic with *Sr7* and was designated *Sr7b* (Loegering and Sears 1966).

In contrast to linkage found by Hayes *et al.* (1934), Waterhouse (1939) reported independent inheritance of the resistances to leaf rust and stem rust. Single dominant factors for resistance to leaf rust were reported in Hope or H-44 or both by Vohl (1938), Ausemus (1944), and Adams (1939). Watson and Luig (1961) showed that Hope and H-44 and their derivatives could differentiate Australian strains of leaf rust.

Mains (1933) reported that a single recessive factor pair conditioned the resistance of Hope to mildew. Wells and Swenson (1944) found single-factor pairs for resistances to leaf rust and mildew in an H-44 derivative and reported that the genes concerned were linked with a recombination value of $20 \cdot 8 \pm 2 \cdot 0\%$.

II. Materials and Methods

Studies on disease reaction were mainly concentrated on Hope, Renown, Spica, and Redman. Table 1 lists their alleged parentages and their known seedling reactions to certain rust strains. H-44 is also included since it occurred in the pedigrees of Renown and Redman. Despite adult plant resistance these cultivars are susceptible in the seedling stage to pre-1954 stem rust strains. A major change in the Australian stem rust flora was first detected in 1954 (Watson and Luig 1966). New strains, which eventually replaced earlier types, were avirulent on Hope in the seedling as well as the adult plant stage. Subsequently variants of the post-1954 strains were found which were virulent on Hope seedlings and showed increased virulence on adult plants.

The cultivars listed in Table 1 react in similar ways to strains of leaf rust between which they distinguish. They also react similarly to, and distinguish between, strains of mildew. Spica was included because its reactions to the different pathogens were similar to Hope derivatives.

TABLE 1

PARENTAGE AND SEEDLING REACTIONS TO CERTAIN STRAINS OF STEM RUST AND LEAF RUST FOR HOPE, H-44, AND THREE CULTIVARS USED IN INHERITANCE STUDIES

R = resistant; S = susceptible; SR = semiresistant

Cultivar	Parentage	Reaction to Stem Rust pre-1954	Reaction to Stem Rust post-1954		Reaction to Leaf Rust	
		126-6,7	21-2	21-5	122-1,2	122-1,2,3
Hope	Marquis × Yaroslav Emmer	S	R	S	R	S
H-44	Marquis × Yaroslav Emmer	S	R	S	R	S
Renown	H-44 × Reward	SR	R	SR	R	S
Spica	(Three Seas × Kamburico) × (Pusa × Flora 3202)	S	R	S	R	S
Redman	*Regent × Canus	S	R	S	R	S

* Regent = H-44 × Reward.

Susceptible cultivars used for inheritance studies in crosses with Renown and Spica included Federation, Morocco, and W2691.* Mentana was also used as a susceptible parent although it possesses the gene *Sr8* for resistance to stem rust. In this case an appropriate *Sr8*-attacking rust strain was used.

A set of single chromosome substitution lines, which involved the replacement of each of the 21 pairs of Chinese Spring chromosomes, one pair at a time, by the corresponding pairs of chromosomes from Hope, was provided originally by Dr. W. Q. Loegering, Beltsville, Maryland, U.S.A., and a monosomic series of Redman by Dr. A. B. Campbell, Winnipeg, Canada.

The definition and nomenclature of rust strains was given by Watson and Luig (1961, 1963, 1966), whilst McIntosh and Baker (1966) described the mildew strain involved.

Infection of seedlings with rust strains was achieved by application of uredospores to leaves with a flat needle, or by shaking uredospores from heavily rusted plants, followed by incubation at high humidity for 24 hr. Inoculation with mildew was carried out by shaking conidia from diseased plants on to seedlings to be tested. In each case notes were taken approximately 14 days after inoculation. Adult plant studies were conducted in the field or, in certain instances, in the glasshouse when inoculations were carried out by spraying with a suspension of rust uredospores in Mobilsol oil.

* W numbers refer to the Sydney University Wheat Accession Register.

III. Results

(a) *Seedling F_2 Studies on Stem Rust Resistance in Spica and Renown W2346*

F_2 seedlings of crosses involving Spica and Renown were inoculated with certain strains of standard race 21. In the case of Renown × Federation strain

Table 2

F_2 segregation to stem rust in certain crosses involving the resistant cultivars Spica and Renown with Federation, Mentana, and W2691

Cross	Strain Used	Plant Number	Resistant	Susceptible	χ^2 Value* (1 : 3 ratio)
Renown × Federation	21-2	1	16	58	0·45
		2	17	53	0·02
		3	18	87	3·46
		4	17	64	0·70
Total			68	262	3·40
Renown × Mentana	21-6	1	14	50	0·33
		2	21	54	0·36
		3	15	50	0·13
		4	18	51	0·04
Total			68	205	0·001
Spica × Mentana	21-6	1	11	32	0·01
		2	33	94	0·07
		3	2	12	0·86
Total			46	138	0·00
$W2691^3$ × Spica	21-2,8	1	8	24	0·00
		3	48	164	0·63
		6	6	25	0·53
		7	22	109	4·70
		9	8	27	0·09
		11	14	127	17·08
Total			106	476	14·30

* Values for significance: 3·84 ($P = 0·05$); 6·64 ($P = 0·01$).

21-Anz-2 (hereafter designated 21-2) was used; for Renown × Mentana and Mentana × Spica strain 21-6, and for $W2691^3$ × Spica strain 21-2,8* was employed.

To each of these strains Spica exhibited a mesothetic ("X^-X") reaction type whilst a more resistant (";1^-") reaction type was characteristic of Renown. To the pertinent strains Federation, Mentana, and W2691 were susceptible exhibiting "3^+4" reaction types.

* 8 refers to virulence on cv. Webster.

Segregation data for reaction types for the above crosses are presented in Table 2. A single recessive gene for resistance is indicated in each instance, although in the case of $W2691^3 \times$Spica the χ^2 values for the total as well as for two of the families tested to this hypothesis are significant. Difficulty in precisely assigning reaction types was experienced in the backcross F_2 population and the significant deviations could have resulted from misclassification.

(b) *Association of Seedling and Adult Plant Resistance to Stem Rust in Spica*

Selected seedlings from segregating F_2 families of the second backcross of Spica to W2691 were transplanted into the field and the mature plant reactions to strain 21-2 noted. Of 47 plants resistant in the seedling stage 46 were resistant as adult plants, whilst all 122 plants from the same populations, susceptible as seedlings, were susceptible in the mature plant stage. The results indicated that the same recessive factor was operative in both seedling and adult plant stages. The exceptional plant was probably due to seedling misclassification.

(c) *Association of Stem Rust and Leaf Rust Resistances in Spica*

In the seedling stage Spica exhibited a characteristic "X" reaction type to leaf rust whilst Morocco was susceptible ("4" reaction type). The behaviour of F_3 lines

TABLE 3

DISTRIBUTION OF F_3 LINES OF THE CROSS MOROCCO × SPICA FOR SEEDLING REACTION TO STRAINS 21-2 OF STEM RUST AND 122-1, 2 OF LEAF RUST

Reaction to Leaf Rust	Reaction to Stem Rust			
	Resistant	Segregating	Susceptible	Total
Resistant	10	5	—	15
Segregating	10	43	6	59
Susceptible	1	8	13	22
Total	21	56	19	96

χ^2 Values		Values for Significance		
		D.F.	$P = 0 \cdot 05$	$P = 0 \cdot 01$
1 : 2 : 1 (stem rust)	2·55	2	5·99	9·21
1 : 2 : 1 (leaf rust)	5·96	4	9·49	13·28
Independence	45·94			

Linkage by F_2 product method $0 \cdot 182 \pm 0 \cdot 045$

of the cross Morocco × Spica to stem rust strain 21-2 and to leaf rust strain 122-Anz-1,2 (hereafter designated 122-1,2) is summarized in Table 3. Single factors were operative against each of the pathogens and the data indicated that the respective resistances were not independently inherited. By the F_2 product method linkage was estimated as $18 \cdot 2 \pm 4 \cdot 5\%$.

(*d*) *Association of Stem Rust and Mildew Resistances in Renown W2346*

Renown was resistant ("01⁻" reaction type) in the seedling stage to mildew strain S.U.2 at temperatures below 20°C. The behaviour of F_3 lines in crosses Renown × Federation and Renown × Mentana to stem rust strain 21-2,6 and to mildew strain S.U. 2 is presented in Table 4. In the case of stem rust, lines homozygous for ";1⁻", ";1⁻,X⁻", or, "X⁻X" reaction types were classified as "homozygous resistant", whilst lines not exhibiting these reaction types were classified as "homozygous susceptible". In "segregating" lines a major recessive gene conditioned

TABLE 4

DISTRIBUTION OF F_3 LINES OF CROSSES RENOWN × FEDERATION AND RENOWN × MENTANA FOR SEEDLING REACTION TO STRAINS 21-2, 6 OF STEM RUST AND S.U. 2 OF POWDERY MILDEW

Cross	Reaction to Stem Rust	Reaction to Powdery Mildew			
		Resistant	Segregating	Susceptible	Total
Renown × Federation	Resistant	34	—	—	34
	Segregating	5	51	4	60
	Susceptible	—	4	33	37
Total		39	55	37	131
Renown × Mentana	Resistant	39	—	—	39
	Segregating	1	100	3	104
	Susceptible	—	2	48	50
Total		40	102	51	193

	Renown × Federation	Renown × Mentana	Values for Significance D.F.	$P = 0\cdot05$	$P = 0\cdot01$
χ^2 (1 : 2 : 1) powdery mildew	3·43	1·88	2	5·99	9·21
χ^2 (1 : 2 : 1) stem rust	1·49	2·42	4	9·49	13·28
χ^2 Independence	194·07	352·11			
Linkage estimate	0·06±0·02	0·025±0·11			

the ";1⁻" and "X" reaction types as suggested for the F_2 data in Table 2. A single recessive factor for mildew resistance was indicated from ratios in segregating lines. In addition the results showed that the resistances were not independently inherited. Using the F_2 product method of estimation, linkage between the genes concerned was calculated to be $6\cdot0\pm2\cdot2\%$ in the case of the cross Renown × Federation, and $2\cdot5\pm1\cdot1\%$ for the cross Renown × Mentana.

(*e*) *Cytogenetic Studies*

Adult plants with single chromosome substitutions of Hope into Chinese Spring were infected with certain post-1954 strains of the stem rust organism which were avirulent on Hope. Substitution lines 6B(X) and 7B(VII) were almost as resistant as Hope, whilst the remaining substitutions and Chinese Spring were susceptible.

Because of the adult plant leaf rust resistance of Chinese Spring no information could be obtained on the chromosome location of Hope resistance to leaf rust.

When the Hope chromosome substitution lines were tested in the seedling stage against stem rust, strain 21-2, lines 6B and 7B exhibited "X^+" reaction types whilst Chinese Spring and the remaining lines showed "3^+" reaction types. Neither 6B nor 7B were as resistant as Hope ("X^-X"). Lines 6B and 7B were also resistant to mildew strain S.U.2. However, in the case of leaf rust strain 135-1,2 seedlings of substitution lines 3B and 7B were more resistant than Chinese Spring. Substitution line 3B was more resistant than Hope and pathogenic tests indicated that it was resistant to all Australian strains of leaf rust, and, therefore, it is considered unlikely that the gene(s) possessed by this line originated from Hope. On the other hand, the leaf rust reaction type of line 7B was similar to Hope suggesting that the gene involved was located on this chromosome.

Hope substitution lines 6B and 7B were morphologically distinct, substitution 6B being awned due to the absence of the awn inhibitor *B2* carried on chromosome 6B of Chinese Spring. When substitutions 6B and 7B were intercrossed all 175 F_2 seedlings studied were resistant to powdery mildew indicating that both substitution lines possessed the same gene for resistance.

Progenies of cytologically identified monosomic plants from 20 different Redman monosomic lines were tested for behaviour to stem rust strain 34-1,2,3,7. With the exception of line 7B all families exhibited a uniform "X^-" reaction type similar to that of Redman. In the case of Redman 7B, segregation occurred for "X^-" and "3" reaction types. When all lines were subsequently inoculated with powdery mildew strain S.U.2, only the stem rust susceptible plants in line 7B were susceptible to mildew.

A number of seedlings from Redman monosomics 6B and 7B were scored for somatic chromosome counts, and inoculated with stem rust strain 34-1,2,3,7. In the case of Redman 7B, all 42 chromosome types were resistant and 41 chromosome types susceptible. All plants of Redman 6B were resistant regardless of chromosome number, indicating that this latter chromosome did not possess the gene conferring resistance.

Since Redman chromosome 7B, but not 6B, bore the genes for resistances to mildew and stem rust, and in view of linkage shown by stem rust and mildew genes, it is unlikely that 6B of Hope possesses a gene for stem rust resistance.

(*f*) *Studies on Varietal Accessions Involving Hope or H-44 Parentage*

A number of wheat cultivars involving Hope or H-44 in their parentage, were tested in the seedling stage with the three diseases. As indicated in Table 5, where results relating to the more important cultivars are presented, many of them possessed seedling resistance to certain Australian strains of stem rust. Notable exceptions in this respect were Rival, Hopps, and Lee; in addition these cultivars did not possess Hope-type mildew resistance, although they were resistant to leaf rust strains which were avirulent on Hope. The cultivar Henry was resistant to stem rust in the seedling stage but susceptible to mildew. All the cultivars shown in Table 5 were resistant to leaf rust; however, a number of those tested, but not included in the table, were susceptible, especially in cases where resistances to stem rust and mildew were also absent.

TABLE 5

SEEDLING REACTIONS OF WHEAT CULTIVARS INVOLVING HOPE OR H-44 PARENTAGE TO CERTAIN STRAINS OF STEM RUST, LEAF RUST, AND POWDERY MILDEW

R = resistant; S = susceptible

Wheat Accession Register No.	Name	Alleged Parentage	Reaction Type to Stem Rust		*sr17** Present (+) or Absent (−)	Reaction to	
			34-1,2,3,7	34-5		Powdery Mildew S.U.2	Leaf Rust 162-1,2
W517	Hope	Marquis × Yaroslav	X^-X	3	+	R	R
W1846	H-44-24	Marquis × Yaroslav	$X^=$	3^-3	+	R	R
W1354	Warigo	Nabawa × Hope	$X^=$	3^-3	+	R	R
W1361	Hofed	Hope × Federation	X^-X	3	+	R	R
W1942	Redman	Regent × Canus	X^-	3	+	R	R
W1943	Regent	H-44-24 × Reward	;1	X^+3	+	R	R
W1991	Glenwari	Nabawa × (Riverina × Hope)	X^-X	3	+	R	R
W2048	Lawrence	Florence × College	X^-	3	+	R	R
W2063	Henry	(Illinois × Hope) × (Webster × Rescue)	;$2^=1^+$	2	+	S	R
W2339	Rival	Ceres × (Hope-Florence)	2	3^-	−	S	R
W2341	Spica	Three Seas × Kamburico	X^-	3^-3	+	R	R
W2346	Renown	H-44-24 × Reward	;1	$23^=$	+	R	R
W1242	Renown	H-44-24 × Reward	2^-2	2^+3^-3	−	S	R
W2462	Aotea	(Hofed × Cross 7) × (Cross 7 × Dreadnought)	X^+	33^+	+	R	R
W2517	Hopps	(Hope × Seafoam)^2 × (Pusa × Flora 3202)	33^+	3^-3	−	S	R
W2547	Gala	Lawrence × Gabo	X^-X	3	+	R	R
W2084	Lee	Hope × Timstein	3^-	;†	−	S	R
W3013	Unnamed	Marquis^5 × Hope (*Sr1*)	3^+	3^+	−	S	‡

* See Section IV. † *Sr11*. ‡ Not tested.

Of a number of Renown accessions tested, all except W1242 behaved similarly to W2346. The latter was used as a differential for the classification of Australian stem rust strains (Watson and Luig 1963). Whilst W1242 did not possess the "X" type seedling resistance to stem rust it appeared to possess an additional gene(s) for resistance which may be present also in Renown W2346. This resistance was of a "2^+3^-" reaction type. The "2" reaction type of Rival was considered to be different from rust reaction types exhibited by Hope and Renown. The "2" reaction type of Henry to strain 34-5 was probably due to a gene derived from its Webster parent.

IV. Discussion

Hope and H-44, and their derivatives, possess at least two types of resistance to different groups of strains of stem rust. To certain post-1954 Australian strains many of these cultivars possess a single recessive gene for resistance which is operative in both seedling and adult plant stages. This factor was found to be located on chromosome 7B and linked with a recessive gene for resistance to mildew, and also with an incompletely dominant gene for leaf rust resistance. The gene for stem rust resistance has been designated as *sr17*, "*s*" connoting its recessive mode in inheritance. It is unlikely that this gene is either *Sr1* or *Sr2* designated by Ausemus *et al.* (1946) because of its recessive behaviour together with failure to locate genes for resistance to stem rust on chromosome 7B in North American studies (Sears, Loegering, and Rodenhiser 1957; Campbell and McGinnis 1957). In addition, no definite linkage between stem rust resistance and leaf rust or powdery mildew resistances have been previously reported. An isogenic *Sr1* Marquis line obtained from Dr. D. R. Knott was susceptible in the seedling stage to strains which were avirulent on Hope.

Table 6

COMPARISON OF SEEDLING REACTION TYPES AND ADULT PLANT REACTIONS OF TWO SINGLE PLANT SELECTIONS OF RENOWN W2346 TO FOUR STRAINS OF STEM RUST

R = resistant; S = susceptible

	Single Plant No.	Strain 34-2,4,5	Strain 21-4,5	Strain 126-1,6,7	Strain 21-2,8
Seedling	3	22+	2+	2+	$X^{=}$
	6	33^{+}	3^{+}	3	$X^{=}$
Adult	3	R	R	R	R
	6	S	S	R	R

In studies on Hope resistance to a pre-1954 strain, Waterhouse (1939) reported absence of linkage between adult plant stem and leaf rust resistances. In our studies adult plants of Hope substitution lines were tested in the glasshouse with strain 126-6,7 [identical with Waterhouse's "race 34" (Watson and Luig 1966)] and all lines, including 6B and 7B, were susceptible, whilst Hope was resistant. Again, certain F_3 lines of the cross Renown × Federation known to possess *sr17* from seedling studies were susceptible to 126-6,7 as adult plants. This demonstrated that *sr17* was ineffective and that genes other than *sr17* were responsible for adult plant resistance to such strains.

Despite the fact that many Australian Hope derivatives were selected prior to 1954, all of these possess *sr17*. Unless its presence resulted from selection for the linked leaf rust or powdery mildew resistances, it may have had some interaction effect on adult plant reaction to earlier strains. Many North American Hope derivatives likewise possess *sr17* which is apparently ineffective against strains in that geographical area.

Renown W2346 was a supplementary stem rust differential cultivar for the Australian and New Zealand geographical area (Watson and Luig 1963). Strains virulent on Hope in the seedling stage are semiresistant ("2,2^{+},3^{-}") on Renown; and

Renown is also resistant in the adult stage to all strains, whereas Hope is semisusceptible to certain of these. However, certain variants of Renown W2346 do not have the additional resistance and their behaviour is identical with that of Hope in the seedling stage. Of six Renown accessions studied all apparently possessed this additional resistance although one of them lacked *sr17*. The differential in current use for classification of the Australian stem rust flora is a variant of Renown W2346 and has been designated "Renown Selection" W3125. Table 6 compares reactions for seedling and adult plants of Renown W2346 single plant selection progenies where single plant 6 represents Renown Selection.

Resistance to powdery mildew in Renown was controlled by a single recessive factor, thus agreeing with the results of Mains (1933). Furthermore, the current studies have shown that mildew resistance is closely linked with *sr17*. Recombination estimates from data for two crosses were approximately 2·5 and 6·0% respectively. We regard these values, particularly the latter, to be inflated because of insufficient plant numbers in certain F_3 lines.

Seedling leaf rust resistance in Spica was controlled by a single incompletely dominant factor which was located approximately 18 recombination units from *sr17*. Wells and Swenson (1944) reported a recombination value of approximately 21% between genes for leaf rust resistance and mildew resistance. Assuming that *sr17* is located between these genes, there is close agreement between their results and those presented herein. The cultivar Henry possessing leaf and stem rust resistances, but not mildew resistance, could then have resulted from a single crossover between the mildew gene and *sr17*. Further, the seedling leaf rust susceptibility of the Hope substitution 6B line could have resulted from a single crossover between *sr17* and the gene for leaf rust resistance. The gene for leaf rust resistance in Hope has been designated *Lr14*.

Law and Wolfe (1966) studied a number of characters controlled by genes on Hope chromosome 7B, including a recessive factor for mildew resistance designated ml^H. In their studies this factor was located on the long arm of 7B, showing approximately 37% recombination with the centromere. Presumably this gene is the same as that located in our studies. In view of the linkages shown, it is therefore very likely that both *sr17* and *Lr14* are also on this arm.

Chromosome 7A carries very closely linked genes for resistance to certain strains of stem rust, leaf rust, and powdery mildew (Watson and Luig 1966). The location of linked genes for resistance to the three pathogens on the homoeologous chromosome 7B might represent a case of parallel evolutionary divergence. However, it is not known whether the genes responsible for the resistances on 7A are located on the arm corresponding to that involved in 7B.

Other cases of linkage of genes for resistance to different pathogens in wheat have been reported. A notable instance is the complete linkage of mildew and stem rust resistances in certain *Triticum timopheevi* Zhuk. derivatives (Nyquist 1963). In two of the three above cases the linked genes have been transferred from species other than hexaploid wheat.

To elucidate further the inheritance of Hope adult plant stem rust resistance, it is proposed to conduct experiments involving simultaneous, isolated rust epidemics caused by different strains on series of F_3 lines from crosses involving Hope and its derivatives. The same lines tested with North American field strains would enable a comparison of results involving strains from different geographical areas.

Results based on the chromosome substitution technique must be carefully considered before conclusions can be drawn, since backcross probabilities allow genes from the donor parent to be carried over on non-substituted chromosomes. This is illustrated by our results with chromosomes 6B and 7B substituted from Hope where supplementary experiments precluded the involvement of chromosome 6B. Obviously this deficiency would be particularly important when investigating polygenic inheritance.

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