RESPONSE OF F4 LINES OF THE CROSSES WICHITA X WEBSTER AND WICHITA X CARINA TO SEVERAL RACES OF LEAF RUST
by

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Leaf rust of wheat, Puocinia triticina Erikss., is one of the most severe diseases attacking wheat and is found in every place in which wheat is grown. Leaf rust has been found to be the most destructive disease of wheat in Kanses. It is estimated that this disease alone reduced the yield of wheat more than $5,431,000$ bushels a year from 1938 to 1952, inclusive. Its damage usually is underestimated because it never totally destroys a Kansas crop and seldom causes severe shriveling of the grains. However, it has been proved that leaf rust reduces the number of kernels per head and the size of the kernels, as reported by Pady, et al.(60)

Leaf rust-resistant varieties offer the chief means of control of this disease. However, the problem of breeding resistant varieties is greatly complicated by the occurrence of many physiologic races of the fungus. At present 163 physiologic races are recognized (49). In addition, Basile (2) has reported the occurrence of 18 new races in Italy.

Eight differential varieties are used to identify these races.

One of the objectives of the wheat breeding program at Kansas Agricultural Experiment Station is to determine the genetic factors present in these differential varieties and to transfer these factors into the hard red winter wheats adapted to Kansas conditions.

This thesis is a part of that study.

## REVIEW OF LITERATURE

The most outstanding review of information on leaf rust of wheat hes been made by Chester ( 8 ), including history, etiology, economic importance, symptoms, physiologic specialization, factors affecting survival and development, and control.

Other papers on the same subject have been published by Fumphrey, et al.(25), Martin and Salmon (54), Dickson (11), and Stakman and Harrar (69).

As far as the technical name of the pathogen is concerned, some arguments have been produced, due to the fact that leaf rust is known by different names. As stated by Chester (8), there are three concepts of the species of wheat leaf rust. One, Puccinia triticina Erikss., limits the species to the leaf rust of wheat; the second concept, P. elymi Westd., or P. clematidis Lagerh. includes in addition leaf rust of grasses. The third concept groups rusts of more than 90 species in 16 genera of grasses into the composite species Puccinia rubigo-vera (D.C.) Wint., which has been subdivided. P. rubigo-vera (D.C.) Wint. f. sp. tritici (Erikss.) Carl., corresponds to Eriksson's Puccinia triticina, term which is preferred by Chester and other investigators.

However, Cummins and Caldwell (10) have recently shown that the oldest valid name applied to forms with 2 -celled teliospores of the leaf rust fungus complex of grasses and small grains is Puccinia recondita Rob. ex Desm., described on rye in 1857. P. elymi should be treated as a distinct species. They also say that other names, such as $P$. rubigo-vera Wint.
(1882), P. perplexans Plowrs. (1885), P. persistens Plowrs. (1889), P. dispersa Erikss. (1894), and P. triticina Erikss. (1899) are later synonyms.

Studies on specialization of leaf rust of wheat started in 1918 ? when Mains and Jackson (53) described the first 12 physiologic races followed by those by Johnston and Mains (43). More recent information has been added by Brown and Johnson (5), Johnson (26), and Johnson and Newton (27). The American species of Thalictrum have no great importance in the production of new races. Leaf rust overwinters in the uredial stage and the only explanation for the great number of races is ascribed to mutation and probably hyphal fusion, as it has been shown for stem rust (75). On the other hand, Chester (8) has reported that in eastern Siberia, the alternate host, Isopyron, is the only means by which the rust can survive from one season to the next.

Peturson, et al.(61) have reported accurate results of studies on the effect of leaf rust on the yield and quality of wheat, showing that heavy infection generally reduces grade while light to moderate infection causes no grade reduction. In the majority of cases leaf rust increases baking strength as measured by loaf volume, and the carotinoid content of the seed is invariable increased by leaf rust infection.

The importance of prevalence and distribution of physiologic races of leaf rust has been emphasized by Chester (9), Fuffman and Johnston (24), and Johnston (37, 38, 41). The situation in South America has been summarized by Vallega (72, 73).

Johnston (38) has stated that:
"evidence is accumulating at Manhattan (Kansas) that environmental conditions have a marked effect on physiologic determination. For example, cultures that appeared to be race 52 during the fall and early winter gave typical reaction for race 5 in the spring when days were longer, light more intense, and temperatures higher. In the same manner, cultures that were typical race 2 in the fall proved to be race 15 in the spring, while cultures that at first appeared to be race 105 later proved to be race 126. Thus there is increasing evidence that some of the described physiologic races are merely ecotypes.

Johnston (41) may be quoted again as follows:
There has been significant changes in the prevalence and distribution of physiologic races of $P$. triticina in the United States during the past 20 years. These changes seem to be related to changes in varieties of wheat. UN 5 has become the most abundant race in the United States, especially in the hard red winter wheat area where Pawnee is the most widely grown variety. UN 6 now is increasing In the same area, where Ponca, Westar, Concho, and Bowle have been distributed recently or have been grown extensively in experimental sowings. UN 10 containing race 11 , long the dominant race on the Pacific Coast and in Mexico, is slowly increasing in the Southeastern and Northeastern States. UN 13 containing the vimulent races 35,54 , and 122 is increasing rapidly, especially in Southeastern States where Chancellor has become an important variety. UN 11 (race 93) has been found erecuently in Southeastern States in recent jears but seldom has been found elsewhere.

Many measures of control of leaf must have been tried, including control by competition with other fungi (Darluca filum), hyperparasitic fungi, predatory insects, and cultural practices, as reported by Chester (8).

Fe also reviewed some of the early experiments with fungicides. Recent experiments have been carried out at Kansas state College by Haskett and Johnston (15) on the chemical control of leaf rust as well as stem must of wheat in Kansas. Their conclusions are as follows:

One or two spray applications of certain fungicides reduced both leaf and stem rust infection in experiments
conducted during the period 1952 to 1955. In some instances losses in yield and reductions in test weight were prevented. Chemical treatments showing some promise were Acti-dione, maneb, zineb, thiram, Karathane, and calcium sulfamate. Zineb, maneb, Acti-dione, and Karathane treatments did not adversely affect the milling and baking quality or seed viability of sprayed wheat, whereas applications of calcium sulfamate resulted in marked reduction of quality and viability. The use of available protective fungicides on a large commercial scale is not recommended in Kansas. However, small fields of valuable seed wheat could be adequately protected.

As stated before, the procuction of resistant varieties offers the best means of control. The nature of the resistance of the appropriate germplasm has been discussed in detail by Chester (8), and Heyne (18).

Methods of breeding have been reviewed by Hayes, et al.(17), and Heyne (18).

In breeding resistant varieties, the knowledge of the inheritance of the resistance is of primary importance. Chester (8) has presented the studies on inheritance of resistance to leaf rust prior to 1940. In general, resistance to leaf rust is inherited in simple Mendelian fashion when hybrids from pure lines of wheat are tested for their reaction to pure rust races. In many cases resistance is governed by a single dominant factor, and in an almost equal number of cases the single factor is recessive. Prequently the single factor is only incompletely dominent or intermediate, so that heterozygous progeny are more resistant that the susceptible parent but more susceptible than the resistant parent. When the rust employed consists of two physiologic races, two resistant factors may be involved, independently inherited, in which case the inheritance follows the simple

Mendelian pattern of a dihybrid cross.
Chester (8) has also reported the early attempts to transfer the resistance from other species of wheat and different genera to common wheat. As early as 1927, Tochinai and Kihara (71) found that certain species of wheat with lower chromosome number, such as Triticum durum, T. turgidum, T. polonicum, T. dicoccum, T. dicoccoides, and T. monococcum, showed high resistance to leaf rust, as well as certain species of Aegilops, such as A. ovata, A. triticoides, and A. squarrosa.

Further studies on inheritance of leaf rust resistance, as well as its correlations with other characters, have shown results similar as those reviewed by Chester (8).

Wells and Swenson (77) studied the F2, F3, and F4 progeny of a cross between a hard red spring wheat selection of H-44Reward $x$ Baringa and a soft white spring wheat selection of Hard Federation $x$ Dicklow for reaction to stem rust, leaf rust, and powdery mildew. Powdery mildew occurred naturally in the nursery. Epiphytotics of the rusts were induced by introducing two prevalent races of stem rust and four of leaf rust. Two or three gene pairs appeared to govern reaction to stem rust. Single gene pairs $L \mathrm{~m} 1 \mathrm{~m}$ and Ms ms appeared to govern reaction to leaf rust and powdery mildew respectively. From analysis for association between genes for reaction to these three diseases, a cross-over value of $20.8+2.0 \%$ was found between the leaf rust and mildew genes. Significant linkage relationships were found for the association stem rust vs leaf rust and stem rust vs mildew, but these two linkages have not been corroborated
by subsequent data from a related cross.
Swenson, et al. (70) found that plants and lines which were highly resistant to leaf must occurred in the progeny of a cross between two susceptible varieties, Thatcher and Triunfo. The segregation obtained in F2 and F3 were fairly satisfactorily explained by postulating two complementary dominant genes, one from each parent. Because there was some indication that one or more modifying genes might be present, an alternative hypothesis involving three gene pairs also was suggested. Under this hypothesis, two genes, non complementary to each other, are contributed by one parent, and these two genes are complementary, either singly or in combination, with one gene contributed by the other parent.

Woodward (84) studied the inheritance of reaction to physiologic races 9,15 , and 58 in two simple wheat crosses, $\mathrm{Ma}-$ lakof $x$ Democrat and Democrat $x$ Mediterranean.

He found that two recessive factors carried by Democrat apparently governed resistance to race 9 of leaf rust.

Malakof carried one factor for resistance to race 15 and one factor for resistance to race 58. Chi-square tests for independence indieated that resistance of Malakof to race 15 and to race 58 was due to the same factor.

Democrat and Mediterranean carried similar factors for their reaction to the three races. Both parents exhibited identical reactions to the three races, being resistant to race 9 , and susceptible to races 15 and 58. All the progeny exhibited reactions identical to those shown by the parents, indicating that the factors for resistance or susceptibility carried by
the two parents were the same.
Martinez, et al. (55), studying the cross Thatcher $x$ (Premier x Bobin-Gaza-Bobin) N.S. No. 11-39-2, found that the inheritance of mature plant reaction to a mixture of leaf rust races in the field was explained as due to the action of three genetic factor pairs independently inherited. Any factor, in the dominant condition, caused susceptibility.

Seedling reaction to races $1,2,5,15,28$, and 128 appeared to be determined by six different genes, one for each race, susceptibility being dominant.

This is one of the cases in which there is a large number of genes responsible for reaction to a rather limited number of leaf rust races, indicating that the inheritance of leaf rust reaction in this particular cross is rather complex. Wu and Ausemus ( 85 ) studied the cross Lee (Ci 12488) x Mida ( CI 12008). Lee is a selection of Hope x Timstein, resistant to leaf rust both in the mature-plant stage to a collection of races and in the seedling stage to 22 individual races. Mida is a selection from a cross of Ceres-Double Cross $x$ Ceres-Hope-Florence, which is a susceptible variety.

Observation in the field indicated that the resistance of Lee in the mature-plant stage to a collection of races was differentiated from the susceptibility of Mida by two pairs of independently inherited genes. These genes were additive in effect and susceptibility appeared to be partially dominant.

Seedling studies of F4 progenies with reference to individual races showed that the resistance of Lee to race 126
was governed by a single recessive factor and to race 5 by a single dominant factor. The Lee factors for resistance to leaf rust races 9,5 , and 126 in the seeding stage, whether dominant or recessive, as well as one of the two factors for mature plant resistance in the fleld, all appeared to be associated in inheritance.

Heyne and Livers (19) studied crosses of 16 different monosomics types of Chinese spring wheat with Pawnee winter wheat, concluding that Pawnee wheat has one major factor for resistance to race 9 of leaf rust located in chromosome $X$. This factor from Pawnee probably interacts with a factor from Chinese to give a two-factor segregation in the seeding stage.

Mode (57) studied the inheritance of leaf rust reaction In seven wheat crosses, Webster $x$ Nediterranean, Carina $x$ Fussar, Carina x Pawnee, Carina $x$ Malakof, Brevit $x$ Hussar, Loros $x$ Pawnee, and Webster x Pawnee: The races used were 5, 9, 15, 19, and 58.

Webster had one dominant factor for resistance to race 5, 15, and 58. Mediterranean had one incompletely dominant factor for resistance to race 9. In the Webster $x$ Mediterranean cross, resistance to races $9,5,15$, and 58 was inherited independently. Carina and Hussar carried different genes for resistance to all races. The Carina reaction to races 5 and 15 was epistatic to the Fussar reaction, when the Carina genes for resistance were homozygous. Carina and Pawnee were differentiated by linked duplicate genes in their reactions to races 5,15 , and 58. Three factors appeared to be involved in the transgressive segregation
for susceptibility to race 15 and high resistance to race 19 In the Carina $x$ Malakof cross tested to these races. Brevit and Hussar carried different genes for resistance to races 9 and 15, apparently associated. The resistance of Loros to race 5 wes differentiated from the susceptiblility of Pawnee by a single incompletely dominant gene.

Fitzgerald, et al.(13) studied the crosses of Purdue 3369, highly resistant soft red winter wheat, with the varieties American Banner, Seneca, Butler, Wabash, Mediterranean, and Malakof. Crosses with American Banner, Seneca and Butler indicated that resistance of 3369 to races $5,9,15$, and 76 was controlled by different single dominant genes and that resistance to race 65 was governed by duplicate recessive genes. Resistance to the other races appeared to be independently inherited.

Genes at two closely linked loci governed resistance to race 9 in crosses of 3369 with both Mediterranean and Wabash, which are also resistant to race 9. The genes for resistance In the latter varieties were recessive and epistatic to the recessive gene for susceptibility, while the dominant gene for resistance in 3369 was epistatic to the dominant gene for susceptibility. Both Malakof and 3369 were found to possess dominant independently inherited genes for resistance to race 76.

Feyne and Johnston (20) studied crosses among Timstein, Pawnee, and RedChief wheats. Timstein spring wheat was found to be resistent in the adult stage to leaf rust races commonly occurring in Kansas, but Pawnee and RedChief winter wheats were found to be susceptible. Timstein was resistant in the seeding
stage, and Pawnee only to race 9. RedChief was susceptible to all races.

Timstein appeared to have one major recessive factor and one or more modifying factors for adult plant resistance: Pawnee had one major factor for resistance to race 9 in the seedling stage that was non-allelic to, and also at least partially epistatic to, the Timstein factor. Timstein had one major recessive factor and one or more minor or modifying factors that controlled the reaction to all races in the seedling stage.

Harris (16) studied the crosses Brevit $\times$ Mediterranean, Carina x Brevit, Webster x Brevit, and Loros x Webster using races 5, 9, and 126. He found that Carina was susceptible to race 9 and Brevit to race 126 in the adult stage, showing a reversal of reaction.

Inconclusive results were obtained in the crosses involving Hussar when tested to races 5 and 35 in the F3 generation and were attributed to environmental conditions. Mediterranean, Hussar, and Democrat were resistant to races 9 and 11 , but segregation occurred in crosses of Fussar $x$ Democrat and Hussar $x$ Mediterranean indicating that Fussar had different factors for resistance from Democrat and Mediterranean. The factors for resistance to races $5,9,11$, and 35 were all associated In the crosses Mediterranean $x$ Hussar and Fussar $x$ Democrat.

Schulte (66) studied the inheritance of reaction to leaf rust in the F3 progeny of the crosses Wichita $x$ Mediterranean, Wichita $x$ Malakof, Wichita $x$ Fussar, and Pawnee $x$ Mediterranean
using races 5,9 , and 15 .
Mediterranean appeared to have one partially dominent factor for resistance to race 9 in the cross Wichita $x$ Mediterranean. Malakof had a single dominant factor for resistance to race 15 in the cross Wichita $x$ Malakof. Hussar had a single partially dominant factor for resistance to both races 5 and 15 in the cross Wichita $x$ Fussar. Mediterranean and Pawnee appeared to have the same factor or factors for resistance to race 9.

Nyquist (59) found that under field conditions, the mature plant resistance of CI 12633 ( strain derived from T. timopheevi ) to race 11 of leaf rust was controlled by one partially dominant major gene in crosses with Federation and White Federation. However, in a cross with Ramona two partially dominant complementary major genes were found.

Chester (8) and Mode (57) have presented lists of varfeties and strains of wheat resistant to leaf must.

Nyquist (59) has stated that to facilitate the development of resistant varieties it would be desirable to have avallable a gene-race handbook. In this, each resistant source should be catalogued with individual races of the pathogen for 1) the number of genes for resistance, 2) the level of resistance of each gene, 3) intragenic interactions, 4) intergenic interactions, and 5) linkage relations.

In an attempt to conform with at least one of the points suggested by Nyquist and other investigators, three tables are presented in this thesis summarizing most of the information available on varieties and strains of wheat found to be resistant
to leaf rust after 1940. Sources of resistance either from other species or genera are also included.

Table 1 shows the varieties, strains, and sources of resistance and the individual races of leaf must to which they have been found to be resistant in the seedling stage. The fourth colum shows the resistance in the adult stage of some of the varieties which have been tested in that stage also. Individual races are not in correlative order: they have been grouped according to authors. Actually, each group contains only additional races because many authors have reported resistance to the same races. References are not given in alphabetic order; they have been arranged according to the jear of the investigation, the last one being, in the majority of cases, the most recent.

In Table 2 are presented some varieties and strains of wheat found to be resistant in tests carried out in the adult stage only, with the correspondent races.

Table 3 shows resistant varieties and strains in the adult stage only, with no races specified. This means that they are or were resistant to the race or races prevalent in one or more locations in the jear concerned.
Table l. - List of varieties or strains of wheat resistant in the seeding stage to specific races

| Name and CI Number | Seedling Stage Races | ! Adult Stage : | References |
| :---: | :---: | :---: | :---: |
| Acme 5284 | 9, 10, 15, 31, 52, 77 | Field | $51,47,44$ |
| Aniversario 12578 | $\begin{aligned} & 3,5,9,14,16,58, \\ & 90,93,126,128 ; 76, \\ & 89 \end{aligned}$ | Field | 51, 64 |
| Aniversario 12956 | $1,3,5,6,9,10,11$, <br> $13,15,19,20,28,35$, <br> 37, $44,54,58,68,84$, <br> 93, 105, 122, 126 |  | 40, 42 |
| Apulia x Progreso 12587 | $\begin{aligned} & 1,2,3,5,9,11,12, \\ & 14,15,16,21,28,31, \\ & 35,43,52,58,90,93, \\ & 107,126,128 \end{aligned}$ | $\begin{aligned} & 5,20,49,57, \\ & 62,114 \end{aligned}$ | 51, 12 |
| Arnautke 1493 | $\begin{aligned} & 1,2,3,5,7,9,10,1 \\ & 11,13,15,16,17,18, \\ & 20,21,28,31,35,49, \\ & 52,58,77,90,93,126, \\ & 128 \end{aligned}$ | Field | $\begin{aligned} & 51,47,44,45, \\ & 46,48 \end{aligned}$ |
| Australith 12808 | 21, 28 |  | 51 |
| Aegilops cylindrice | 1, 6, 37 |  | 23 |
| Aniversario $x$ Frontana PS | 76,89 |  | 64 |
| Aniversario $x$ Exchange F 4 | 76, 89 |  | 64 |
| Aguilera-Kenya 324 (Marroqui Supremo) Kentana | 1, 6, 32, 126 |  | 3 |

Table 1. - (continued)

| Name and CI Number | $\begin{aligned} & \text { Seedling Stage } \\ & \text { Races } \end{aligned}$ | Adult Stage | References |
| :---: | :---: | :---: | :---: |
| Arabian PI 145720-10 | $\frac{1}{5}, 5,6,9,15,21,32,$ 122, 126, Mixture 122, $126,93,105,105 \mathrm{~B}$, | Field | 3, 52 |
| Austin 12288 | 2, 9, 12, 45 | Field | 65,47 |
| Baart - $1121 \times 1581$ | 1, 2, 7, 15 |  | 51 |
| Bahtense 12591 | 28, 93 |  | 51 |
| Benvenuto Inca 12588 | 1, 5, 11, 28 |  | 51 |
| Benvenuto Pampa 12809 | 1, 5, 9, 11, 28 |  | 51 |
| Barbaro Portugal 789 | 3, 11, 73, 87, 143 |  | 14 |
| Blackhull-Oro x Pawnee | 2, 5, 9, 12 |  | 65 |
| $\text { Blackhu11-Oro x Pawnee } 43 \mathrm{hl} \text { Wd }-389$ | 2, 5 |  | 65 |
| $\text { Blackbull-Oro x Pawnee } 43 \mathrm{hl} \text { Wd }-89$ | 9, 65 |  | 65 |
| Blackhull-Oro x Pawnee - 94 | 9, 65 |  | 65 |
| Blackhull-Oro x Pawnee - 236 | 9, 65 |  | 65 |
| Bowie 13146 | $\begin{aligned} & 1,3,6,9,10,11, \\ & 33,19,37,44,688 \\ & 84,93,20,105,131 \end{aligned}$ |  | 40, 42 |
| Bowle 3702-22 (Texas) | 9, 11, 15, 32, 93, 105 |  | 52 |

Table 2 - (contimued)

|  | I Number | $\begin{gathered} \text { Seedling Stage } \\ \text { Races } \\ \hline \end{gathered}$ | Adult Stage | References |
| :---: | :---: | :---: | :---: | :---: |
| Blackhull |  | 10 |  | 42 |
| Blackhawk | 12218 | $\begin{aligned} & 9,11,45,93,105, \\ & 128 ; 15,20 \end{aligned}$ | Pield | 42, 47, 44 |
| Bajio 53 | (Mexico) | 9, 58 | Field | 3 |
| Baart 46 | 12346 | 1, 5, 105 |  | 3 |
| Beladi | 7265-5 | 1, 5, 9, 15 |  | 3 |
| Barrigon 5 |  | 1, 9, 15, 32, 126 | Field | 3 |
| Beladi 116 | PI 192589 | $\begin{aligned} & 5,6,9,15,32,93, \\ & 105,122 \end{aligned}$ |  | 52 |
| Cadet | 12053 | $\begin{aligned} & 1,2,3,5,7,9,11, \\ & 15,20,26,28, \end{aligned}$ | Field | 51, 47 |
| Capellı | 121452 | $\begin{aligned} & 1,2,3,5,7,9,10, \\ & 11,12,13,14,15, \\ & 16,17,18,21,28, \\ & 31,35,43,49,52, \\ & 58,77,90,93,107, \\ & 126,128 \end{aligned}$ | Field | $\begin{aligned} & 51,29,30, \\ & 31,32 \end{aligned}$ |
| Carleton | 12064 | $\begin{aligned} & 1,2,3,5,7,9,10, \\ & 11,13,14,15,16, \\ & 17,18,20,21,28, \\ & 31,33,35,49,52, \\ & 77,90,93,126 \end{aligned}$ | Field | $\frac{51}{45}, 47,44,$ |

Table 1. - (continued)

| Name and CI Number | $\begin{gathered} \hline \text { Seeding stage } \\ \text { Races } \\ \hline \end{gathered}$ | Adult Stage : | References |
| :---: | :---: | :---: | :---: |
| Centenario 12021 | $\begin{aligned} & 1,2,3,5,9,11,12, \\ & 14,15,16,20,26, \\ & 26,31,33,49,58, \\ & 61,107,126 ; 6,68, \\ & 93,105,122 \end{aligned}$ | 57, 62 | $51,42,12$ |
| Cincena 12810 | $\begin{aligned} & 2,5,11,13,28,90, \\ & 93 \end{aligned}$ |  | 51 |
| Cartiela 3 (Portugal 1131) | 3, 11, 73, 87, 143 |  | 14 |
| $\begin{gathered} \text { Comanche } \\ \text { Eard Fed } \\ \text { Blackhull } \\ \text { L/h2 } 2-187 \end{gathered}$ | 2, 5, 9, 12, 45 |  | 65 |
| Comanche x Cheyenne - Blackhull | 6, 9, 12 |  | 65 |
|  | 2, 5, 12 |  | 65 |
| $\begin{gathered} \text { Comenche X Cheyenne - } \\ \text { Blackhull } \\ 43 \mathrm{~h} 3^{\text {Wd }}-85 \end{gathered}$ | 2, 6, 9 |  | 65 |
| $\begin{gathered} \text { Comenche } \\ \text { Xlackhull Cheyenne } \end{gathered} \underset{43 \text { h3 }{ }^{\text {Wd }}-81}{ }$ | 2, 9 |  | 65 |
| Comenche x Blackhull - Ward Fed $43 \mathrm{~h} 2^{\text {Wd }}-315$ | 2,12 |  | 65 |
|  | 2 |  | 65 |
| Cheyenne x Turkey | 9 |  | 65 |

Table 1. - (continued)

Table 1. - (continued)

| Name and CI Number | $\begin{gathered} \hline \text { Seedling Stage } \\ \text { Races } \\ \hline \end{gathered}$ | Adult Stage | References |
| :---: | :---: | :---: | :---: |
| Einkorn 2433 | $\begin{aligned} & 1,2,5,6,8,9,12, \\ & 12,14,15,16,20, \\ & 21,31,33,35,43, \\ & 44,49,50,52,60, \\ & 64,90,93,126,128 ; \\ & 11, \mathrm{U}, \mathrm{NN.14,} \mathrm{32,58,} \\ & 89,105,122, \text { Mixt. } \end{aligned}$ |  | 51, 52 |
| Esteana 12811 | $\begin{aligned} & 9,11,13,14,16,28, \\ & 31,93,128 \end{aligned}$ |  | 51 |
| Eureka (Argentina) 12812 | 93 |  | 51 |
| Exchange 12635 | $\begin{aligned} & 1,2,3,4,5,7,9, \\ & 11,12,14,15,16,17, \\ & 19,21,28,31,33,35, \\ & 37,40,43,52,58,77, \\ & 90,91,93,105,107, \\ & 126,128 ; 76,89 \end{aligned}$ | $\begin{gathered} \text { Field } \\ (18 \text { races }) \end{gathered}$ | $\begin{aligned} & 51,64,63, \\ & 4,29,31,32, \\ & 33,34,35 \end{aligned}$ |
| Egipto (Portugal: 4 sels.) | 3, 11, 73, 87, 143 |  | 14 |
| Egypt $101 \times$ H143 12792 | 5,15,58 | Field | 78 |
| Etoile de Choisy PI 193108 | 5, 6, 15, 105, 122 |  | 42 |
| Egypt No 101 x Timstein | $\frac{1,5,9,15,21,32,}{105}$ |  | 3 |
| $\text { Egypt No } 101-\frac{\text { Timstein })(\text { Mexico })}{\text { x Mayo }}$ | $\frac{1}{5}, 5,9,15,21,32,$ $58,105,126 ; 93,122$ |  | 3, 52 |

Table 1. - (continued)

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Table 1. - (continued)

Table 1. - (continued)

| Name and CI Number | $\begin{aligned} & \hline \text { Seedling stage } \\ & \text { Races } \\ & \hline \end{aligned}$ | : Adult Stage | Reforences |
| :---: | :---: | :---: | :---: |
| Garnet x Kenya 58 PI 234168 | U N 14, 15 |  | 52 |
| Haynes Bluestream 2874 | $\begin{aligned} & 1,5, \frac{11,}{5}, 15,28, \end{aligned}$ |  | 51 |
| Henry 12265 | $\begin{aligned} & 1,2,3,5,7,9,10, \\ & 11,12,14,15,16, \\ & 20,21,26,28,33, \\ & 43,49,58,61,90, \\ & 91,107,126 ; 6,105 ; \\ & 105 \mathrm{~A} \end{aligned}$ |  | 51, 42, 3 |
| Hope 8178 | $\begin{aligned} & 3,11,13,12,35,44, \\ & 52,58,64,93 \end{aligned}$ | Field | 51, 47 |
| Hamira A C 5 Portugal 9860 | 3, 11, 73, 87, 143 |  | 14 |
| Hard Federation hybrid | 2, 5, 9 |  | 65 |
| Hard Federation - Kawvale x Med. - Hope | 5, 9, 65 |  | 65 |
| Hardired 47-12 | 5, 9, 19, 58, 93, 126 |  | 42 |
| (Henry $x$ Khapli) $x{ }_{(\text {CI } 12633 \times \text { Hope) })^{2 \text { (Texas) }}}$ | $\begin{aligned} & 5,6,11, \text { U N } 14,21, \\ & 32,58,89,93,105 \text {, } \\ & \text { M1xtures } \end{aligned}$ |  | 52 |
| $\begin{aligned} & \text { (III. No. 1-Chinese) }{ }^{2} \pi \\ & \text { Timopheevi (Wisc. } 245 \text { ) } \\ & 12633 \end{aligned}$ | $\begin{aligned} & 9,11,12,14,15,16, \\ & 58,126 \end{aligned}$ | Field | 51, 31, 32 |
| Italian PI 210880 | $\begin{aligned} & 5,6,9,15,105, \\ & 122 \end{aligned}$ |  | 42 |

Table 1. - (continued)

| Name and CI Number | Seedling stage |
| :--- | :--- | :--- | :--- |
| Races |  |

Table 1. - (continued)

Table 1. - (continued)

| Name and CI Number | $\begin{gathered} \text { Seedling Stage } \\ \text { Races } \\ \hline \end{gathered}$ | : Adult Stage | $!$ | References |
| :---: | :---: | :---: | :---: | :---: |
| Lee 12488 | $\begin{aligned} & 1,2,3,4,5,6,7, \\ & 9,11,13,14,15, \\ & 16,17,19,21,28, \\ & 31,33,35,37,40, \\ & 43,49,50,52,58, \\ & 64,77,90,91,93, \\ & 105,107,126,128 ; \\ & 26,95 ; 22 \text { races; 10, } \\ & 44,54,84,122 ; 20, \\ & 32,89, \end{aligned}$ | $\begin{aligned} & \text { Field } \\ & \text { (Mixt.) } \end{aligned}$ |  | $\begin{aligned} & 51,76,85, \\ & 40,42,52, \\ & 4,29,33,34 \end{aligned}$ |
| La Prevision - $25 \times 72817$ ( $=$ Trumbull - Red Wonder Timstein) | 58, 122 | 58, 122 |  | 1 |
| La Prevision $x$ Exchange | 58, 122 | 58, 122 |  | 1 |
| La Prevision x Klein Titan | 58, 122 | 58, 122 |  | 1 |
| La Prevision $x$ R.L. 2327 <br> ( $=$ McMurahy - Exchange - Redman) | 58, 122 | 58, 122 |  | 1 |
| La Prevision $x$ Exchange $\mathrm{F}_{4}$ | 76,89 |  |  | 64 |
| La Prevision $x$ Aniversario $\mathrm{F}_{4}$ | 76,89 |  |  | 64 |
| La Prevision $x$ Frontana $\mathrm{F}_{2}$ | 76, 89 |  |  | 64 |
| Lerma 52 (Mexico) | 1, 105B |  |  | 3 |
| Lerma Rajo (Mexico) | 11, U N 14, 58, 93, 122 |  |  | 52 |
| Langdon, Ld 37213165 | 89, 93 |  |  | 52 |

Pebie I. (continued)

Table 1. - (continued)

| Name and CI Number | $\begin{gathered} \text { Soeding Stage } \\ \text { Races } \\ \hline \end{gathered}$ | Adult Stage : | Reforences |
| :---: | :---: | :---: | :---: |
| Marquillo - Oro x Pawnee | 9 |  | 65 |
| $\text { Mediterranean - } \begin{gathered} \text { Hope } x \\ \text { Pawnee } \end{gathered} \quad 12287$ | 9 | Field | $65,47,44$, 45,46, |
| Maria Escobar $\quad \begin{aligned} \text { PI } \\ \end{aligned}$ | ${ }^{1} 8,5,84,93,93,122,58$, | Field | $\begin{aligned} & 42,3 \\ & 34,35 \end{aligned}$ |
| Maretts M925 | ${ }_{5}^{9} 8,11,9315,19,45$, |  | 42 |
| Magnif a PI 197663 | 1, 9, 58 | Field | 3 |
| Maria Escobar ${ }^{2}$ x Newthatch | 1,5,6, 15, 58 |  | 3 |
| Mayo 52 (Mexico) | ${ }_{105}^{1,5,9,15,21,58,}$ |  | 3 |
| Mayo 52A (Mexico) | 1, 9, 21, 105 |  | 3 |
| Mayo 54 (Mexico) |  |  | 3, 52 |
| (Mida - Maria Escobar) x <br> (Egypt 101 - Timstein) | 1, 32, 105 A |  | 3 |
| Magnif Disro PI 220443 | UN $14,89,93$, Mixt. |  | 52 |
| Mida-Mellurachy - Exohange (Minn.) | U N 14, U N 17, 32 Mixtures |  | 52 |
| Marla Escobar ${ }^{2} \times$ McNurachy 234174 | 11 , $\mathrm{O} \mathrm{N} 12, \mathrm{~J} \mathrm{~N} 14,58$, <br> 93, 122, Mixtures |  | 52 |

Table I. - (continued)

Table 1. - (continued)

| Name and CI Number |  | : Seedling Stage Races | : Adult Stage | References |
| :---: | :---: | :---: | :---: | :---: |
| Pelon Plateado | 12819 | 1, 9, 11, 15, 28 |  | 51 |
| Pentad | 3320 | 5, 9, 21, 52, 126 |  | 51 |
| Petiso | 12820 | 1, 5, 9, 11, 15, 28 |  | 51 |
| Pilot | 11945 | $\begin{align*} & 1,2,3,5,6,7,9, \\ & 11,15,20,26,28, \\ & 40,50,58,64,90,91 \end{align*}$ |  | 51 |
| Pilot $\times 1514$ | 12476 | $\begin{aligned} & 1,2,5,6,11,17, \\ & 31,40,50,91 \end{aligned}$ |  | 51 |
| Premier | 11940 | $1,2,3,12,16,31,$ | Field | 51, 47 |
| Premier x Bobin ${ }^{2}$ - Gaza | 12821 | $\begin{aligned} & 1,2,3,5,6,7,9, \\ & 11,12,13,14,15, \\ & 16,17,21,28,31, \\ & 35,40,43,49,50, \\ & 52,58,64,77,90, \\ & 91,93,107,126,128 ; \\ & 128 \text { a } \end{aligned}$ | Field | 51,55 |
| Purdue 3369 |  | 5, 9, 15, 65, 76 |  | 13 |
| Pawnee $x$ Oro |  | 9, 65 |  | 65 |
| Pawnee (early selection) |  | 9, 65 |  | 65 |
| Pawnee | 11669 | $\begin{aligned} & 1,9,10,11,13,19, \\ & 37,68,84,93 ; 31,65 \end{aligned}$ | Fleld | $\begin{aligned} & 40,42,9, \\ & 19,20,65 \end{aligned}$ |

Table 1. - (continued)

Table 1. - (continued)

Table 1. - (continued)

Table 1. - (continued)

| Name and CI Number | $\begin{gathered} \text { Seedling Stage } \\ \text { Races } \\ \hline \end{gathered}$ | : Adult Stage | References |
| :---: | :---: | :---: | :---: |
| Supremo 12531 | $\begin{aligned} & 1,32,58,105,105 \mathrm{~A}, \\ & 126 \end{aligned}$ | Field | 3 |
| Supremo 51 (Mexico) | 1, 9, 32, 105A, 126 |  |  |
| St 464 PI 191365 <br>  CI 13160 | $\begin{aligned} & 1,5,9,58,105 \mathrm{~B} ; 15, \\ & 21,89,93,105,122, \\ & \text { Mixt. } \end{aligned}$ | Field | $3,52,34,$ |
| Sloux | 1, 9, 10, 11, 15, 93 |  | 42 |
| Surpresa $x$ (KenyaGular) 3707-9-7 | 5, 9, 15, 93, 122 |  | 52 |
| Do 3707-39-4 (Texas) | $\begin{aligned} & 5,9,15,21,32,58, \\ & 93,122 \end{aligned}$ |  | 52 |
| Do 3707-87 (Texas) | 5, 9, 15, 32, 93, 122 |  | 52 |
| Shands 473 x Cheyenne, (Kansas) 55R 7858 | 9, 11, U N 14, 89 |  | 52 |
| Selkirk, CT 232 (Canada) | $5,9,11$, U N 14,15 , $21,58,89,93,105$, 122, Mixt. |  | 52 |
| Thatcher 10003 | 44 |  | 51 |
| Thew 5002 | 1, 58, 91 | 5, 20 | 51, 12 |
| T. timopheevi 11802 | $\begin{aligned} & 1,2,5,9,11,12, \\ & 14,15,16,20,21, \\ & 26,28,31,33,35, \\ & 43,49,52,58,61, \\ & 90,93,107,126, \\ & 128 \end{aligned}$ | Field | $51,47,44$, $45,46,48$, $28,29,30$, $31,32,33$, 34 |

Table 1. - (continued)

| Name and CI Number | $\begin{gathered} \text { Seedling stage } \\ \text { Races } \\ \hline \end{gathered}$ | : Adult Stage : | References |
| :---: | :---: | :---: | :---: |
| T1mstein 12347 | $1,2,3,5,9,11$, <br> $14,15,16,20,21$, <br> $26,28,33,35,52$, <br> $58,90,93,126,128 ;$ <br> 32, 105; 89, 122, <br> Mixt; 4 $4,126,95$ | Field | $51,42,3,$ |
| Timstein x Newthatch 12634 | $\begin{aligned} & 1,2,3,5,7,9,11, \\ & 12,13,14,15,16, \\ & 21,28,31,35,43, \\ & 52,58,90,93,107, \\ & 126,128 \end{aligned}$ |  | 51 |
| $\frac{\text { T. timopheevi }}{\text { Sel. } 26} 66 \text { wheat } 12633$ | Many races (11 are mentioned) | Field | 59 |
| Trintecinco $\times$ Litoral 12823 | 7, 13, 31 |  | 51 |
|  | 21 | 21 | 74 |
| T. monococcum var. vulgare | 1, 6, 37 | 32, Field | 23, 71 |
| T. monococcum (early) mutant | 1, 6, 37 | 32 | 23 |
| T. monococcum var. flavescens | 1, 6, 37 | 32 | 23 |
| T. polonicum var. vestitum | 1, 6, 37 | 32 | 23 |
| Tennessee 47-1-20 | 5, 58, 122 | Field | 79 |
| T. timopheeri x steinwedel $\text { W. } 1309$ | 29, 95, 135, 138 |  | 76 |

Table 1. - (continued)

| Name and CI Number | $\begin{gathered} \text { Seedling Stage } \\ \text { Races } \\ \hline \end{gathered}$ | Adult Stage : | References |
| :---: | :---: | :---: | :---: |
| $\left(\begin{array}{cc} \text { (T. vulg. } & \left.\times \frac{\text { T. timo.) }}{x} \quad \begin{array}{c} \text { (Several } \\ \text { Sels. } \end{array}\right) \end{array}\right.$ | $\frac{1}{19,}{ }^{\text {a }} 37,10,68{ }^{11, ~ 13,}$ |  | 40 |
| Titan | $\begin{aligned} & 1,3,5,6,9,10, \\ & 11,15,19,20,21, \\ & 28,35,37,45,50, \\ & 58,77,93,105, \\ & 122,126 \end{aligned}$ | 5, 20, 49, 67, | 42, 12 |
| Travis | $\begin{aligned} & 1,3,5,9,10,13, \\ & 15,35,93,122 \end{aligned}$ |  | 42 |
| T. polonicum | ${ }_{4} 4_{4} 6,13,15,19,37$, |  | 42 |
| Timstein $\times$ Kenya |  |  | 3 |
| Timstein x Kenya ${ }^{2}$ | 1, 9, 21, 32, 58, 105A | Field | 3 |
| Toluca 54 (Mexico) | 1, 32, 126 |  | 3 |
| Timstein $\times$ Henry 13026 | $\begin{aligned} & 1,5,6,9,15,21, \\ & 32,58,105,105 \mathrm{~A}, \\ & 105 \mathrm{~B}, 126 \end{aligned}$ | Field | 3, 33 |
| Tremez Molle CI 7067-1-1c | $\begin{aligned} & 1,5,6,9,15,21, \\ & 32,58,105,105 \mathrm{~A}, \\ & 105 \mathrm{~B}, 126 ; 11,89, \\ & 93,122, \text { Mixt. } \end{aligned}$ | Field | 3, 52, 7 |
| Tremez Preto 7065 | $\begin{aligned} & 1,5,6,9,15,21 \text {, } \\ & 32,58,105,105 \mathrm{~A}, \\ & 105 \mathrm{~B}, 126 \end{aligned}$ | Field | 3, 7, 4 |

Table 1. - (continued)

Table 1. - (concluded)


Table 2. List of varieties and strains of wheat resistant only in the adult stage to specific races of leaf rust.


Table 3. Varieties and strains of wheat reported as resistant to leaf rust in the adult stage without reference to reces.

| Name and C. I. number | : References |
| :---: | :---: |
| Hard Federation x Dicklow | 77 |
| Thatcher $x$ Triunfo (Transgressive seg.) | 70 |
| Coker 47-27 | 79 |
| M 12-32 | 56 |
| Vencedor | 56 |
| Portugal $\begin{array}{r}65 \\ \\ 90\end{array}$ | 56 56 |
| Uruguey 386 | 56, 4 |
| " 392 | 56 |
| El Milagro | 56 |
| Minor | 56 |
| Argentine | 56 |
| Bladette de Besplas | 56 |
| Contenario, Ks 38. F.N. 4002 | 7 |
| Portuguez ( 2 sels, ) 7012 | 7 |
| Rafaela ( 6 sels.) | 7 |
| Renacimiento, Ks 38. F.N. 88 | 7 |
| Ribeiro sel | 7 |
| Aza de Corvo 7053 | 7 |
| Da Terra ( 2 sels.) | 7 |
| Monjil No. 22 ( 2 sels.) | 7 |
| Chinese 6223 | 4, 47 |
| Illinois No. 1 No 8 | 4 |
| Chinese $2 \times$ T. timopheevi | 4 |
| Klein Aniversario | 4 |
| Redman x Frontana | 4 |
| Surpresa x Kenya C 4913 | 4 |
| Supremo x ( Kenya C 9906) 2 | 4 |
| (T. dicoccoides $\times$ Ae. speltoides) $\times$ Austin 2 | 4 |
| Lee x Frontana | 4 |
| Sando R.N. 52 | 4 |
| Peru - Supremo | 4 |
| (Mentana - Peru ) x Kenya | 4 |
| ( Mayo-Peru-Supremo x $\times$ Peru-Kenya | 4 |
| Kenya-Marroqui $2 \times$ Peru | 4 |
| N.S. III - 51-34 | 4 |
| S.H. 170 (Pullman) | 4 |
| S.H. 198-4 (Pullman) | 4 |
| $P_{\text {in }} W^{276} \text { (Sakatoon) }$ | 4 |
| " 327 " ${ }^{\text {" }}$ | 4 |
| T. vulgare $x$ Agropyron elongatum | 62 |

Table 3 (Cont.)

| Name and C.I. number |  | References |
| :---: | :---: | :---: |
| Chinese $x$ A. elong. $x$ Purplestraw $x$ |  |  |
| Red Rock $x$ Comet $x$ Red Rock |  | 62 |
| Chinese $x$ rye $x$ Chinese $x$ A. elong. $x$ chen |  |  |
| Rising Sun $x$ Purplestraw and Leapla | (2 sels) | 62 |
| Chinese $x$ rye $x$ Chinese $x$ |  |  |
| A. elong. $x$ Forward (2 sel |  | 62 |
| Chinese X A. Elong. X Harvest Queen |  |  |
| and Purplestra |  | 62 |
| Rising Sun $x$ A. elong, x IlliniChief x |  |  |
| Chinese $x$ A. elong. $x$ Arlando and |  |  |
| H - 44 | 8177 | 47 |
| Merit | 11870 | 47 |
| Kubanka 75 | 1154.1 | 47 |
| Pentad | 3320 | 47, 44, 46 |
| Akrona | 6881 | 47 |
| Webash | 11384 | 47 |
| Fultz sel x fungarian sel | 11849 | 47 |
| Do | 11850 | 47 |
| Do | 12017 | 47, 44 |
| Trumbull $\times$ Fultz sel | 12217 | 47, 44 |
| Do | 12220 | $4{ }_{4}$ |
| Hope $x$ fussar | 11682 | 47 |
| " x Kawvale | 11959 | 47 |
| " x Mediterranean | 11763 | 47 |
| Marquillo x Oro | 11851 | 47 |
| Do | 11979 | 47 |
| Red Rock x Hope | 11821 | 47 |
| Hope x Cheyenne 11969 47 |  |  |
| Comanche x ( Med.-Hope) | 12329 | 44, 45, 46 |
| (Kaw.-Marq.) x Tenmarq | 12330 | 44 |
| (Marq.-Oro) x (Oro-Tenmarq) | 12406 | 45, 48 |
| Do | 12407 | 45, 46, 48 |
| Oro x ( Med.-Hope) | 12460 | 46, 48, 28 |
| Trumbull $\times$ Frondoso | 12531 | 48 |
| Do | 12461 | 28, 29 |
| Trumbull x ( W 38-Fultz-Fung. 128) | 12530 | 29,30 |
| Ld $216 \times$ Ld 240 | 12622 | 30 |
| Ld 2ll x Ld 217 | 12621 | 30, 32 |
| Wabash x American Benner | 12757 | 30,32 |
| ( C.I. 12217 ) x Minhardi-Wabash-Purplestraw-Chinese, ete. | 12749 | 30 |
| Leapland x Fronteira | 12536 | 30, 31, 32 |
| Ill, I-Chinese $2 \times$ T. timopheevi | 12632 | 31 |
| Frontana x ( 2265-Redman )2 | 12910 | 31 |
| From Palestine | 12898 | 32, 33, 34 |

Table 3 (Cont.)

| Name and C.I. number |  | References |
| :---: | :---: | :---: |
| Frondoso-Fultz $\times$ Trumbull- <br> W $38-\mathrm{Fultz}$ sel-Hung. |  |  |
| Frontane x Thatcher II-46-53 | 13099 | 33 |
| R.L. $2265 \times$ Redman 3 , CTI 86 | 13100 | 33 |
| Feirfield x ( Trumbull2- |  |  |
| ( ( I 12217) x Minh, Wabash- | 13089 | 33 |
| Purplestraw-Chinese-Mich.Amber | 12798 | 33 |
| ( Comanche x Med, -Hope) x Chiefkan | 12801 | 33 |
| Cheyenne ) xWichita | 12703 | 33 |
| Minturki x Timstein-vulgare2 | 13091 | 33 |
| Lee $x$ Mida | 13152 | 34 |
| Do | 13153 | 34 |
| Frontana x Kenya 58-NewthatchDoDo | 13154 | 34, 35, 36 |
|  | 13155 |  |
|  | 13241 |  |
| Lee $\times$ Frontana | 13201 | 35, 36 |
| Ramsey, Id 369, Carleton x P.I. 94701 | 13246 | 35, 36 |
| Towner, Ld 370R.L. 3206 | 13247 |  |
|  | 13141 | 35, 36 |
| R.L. <br> R.L. 3206 <br> 1007 | 13142 | 35, 36 |
| Chinese2 x A. elong.) x Pawnee (Wheat-rye $\bar{x} \frac{1}{\text {. elong. }} \mathrm{x}$ Cheyenne | 13113 |  |
|  | 13114 |  |
| Shands 473 x Cheyenne | 13005 | 35 |
| Minturki $x$ ( Ill,-Chinese $x$ timopheevi) Red Turkey) x Blackhawk | ${ }_{1} \times 1225$ |  |
|  | 13225 |  |
| $\frac{\text { Triticum-A, elong, }}{\text { Furdue } 4548 \text { A } 2-5-18}$ Pawnee | 13020 | 35, 81 |
|  | 13170 | 35, 36 |
| (Wabash-Amer-Banner) x Aniversario | 13227 |  |
| Trumbull-A. elong, $x$ fultz sel-Trumbull-Hope-Hussar | 13228 | 35, 36 |
| Comanche $\times$ La Prevision 25$\mathrm{~K} 338 \mathrm{AA} \times \mathrm{N} . \mathrm{S}$. $3880.191, \mathrm{~A}$ | 13229 |  |
|  | 13075 |  |
| Knox ( from Chinese) |  | 80 |
| Saline |  | 80 |
|  |  | 80 |
| Fairchild |  | 80 |
| Butler |  | 80 |
| Dual | 13083 | 80 |
| Thorne <br> (Kawvale-White Fed.-Early Premium) x (Clarkan-Med) |  | 80 |
|  |  | 80 |
| Vermillion |  | 81 |
| Bledsoe |  | 81 |

Table 3 (Concl.)

| Name and C.I. number |  | : Re |
| :---: | :---: | :---: |
| Cornell sel. 82 al-2-4,7, |  |  |
| (from a wheat-rye cross) | 13078 | 82 |
| Kent ( = Trumbull-Hope- |  |  |
| - Hussar) $x$ Dewson's |  | 83 |
| Med.-Hope-Pawnee x <br> Oro-Illinois No. 1 - Comanche |  |  |

## MATERIALS AND METHODS

The seedling reaction of $F 4$ progeny of the crosses Wichita $x$ Webster and Wichita $x$ Carina was tested in the greenhouse with races $5,9,15$, and 105 of leaf rust during the winter of 1957-58.

There were 214 lines of Wichita $x$ Webster and 207 Ilnes of Wichita $x$ Carina studied, each line representing seed of one F2 plant. These were not random samples of each cross and ratios could not be determined from the data obtained. The principle objective was to test lines homozygous for race 15 to several other races.

The tests were conducted in an isolated section of the greenhouse with one race of rust at a time. Arter completing a test with a given race, the greenhouse section was thoroughly cleaned to avoid contamination with the new race introduced.

The pure cultures of races 5, 9, 15, and 105 used in the experiments were obtained from Mr. C.O. Johnston, Pathologist, ס.S. Department of Agriculture, stationed at Kanses State College.

The method of innoculation was the same used and described by Woodward (84), Mode (57), Harris (16), and Schulte (66). Approximately 25 seeds of each line were sown in 3 -inch pots. Ten days after planting, the seedlings were innoculated with a pure culture of the desired physiologic race of leaf rust which had been propagated on the susceptible variety Cheyenne. The plants were then placed in a canvas moist chamber, moistened, and dusted with urediospores from the infected Cheyenne plants, using at least 12 pots of infected plants to be sure of a complete innoculation. One set of 100 F 4 lines, with appropiate
differentials to detect race mixtures, was innoculated each two days. Pots were removed from the moist chamber approximately 12 hours after innoculation and watered every day.

In 10 to 12 days, depending on temperature and light intensity, the plants were classified as to phenotype on the basis of type of uredia formed in six classes described by Mains and Jackson (53), and Johnston and Mains (43) as follows:

0 Highly resistant - No uredinia formed: small flecks, chlorotic or necrotic areas more or less prevalent.

1 Very resistant - Uredinia few, small always in small necrotic spots. More or less necrotic areas produced without development of uredinia.
2 Moderately resistant - Uredinia fairly abundent, of moderate size, always in necrotic or very chiorotic spots. Necrotic spots without uredinia.

3 Moderately susceptible - Uredinia fairly abundant, of moderate size. No necrosis produced, but sometimes slight chlorosis immediately surrounding the uredinia.

4 Very susceptible - Uredinia abundant, large. No necrosis or chlorosis immediately surrounding the uredinia. Infected areas sometimes occurring as green islands surrounded in each case by a chlorotic ring.
$X \frac{\text { Intermediate }}{\text { same leaf. Two or more type reactions on the }}$
One of the parents and the other differentials used as checks reacted to the races used as expected, that is, their seedling reaction corresponded to those given to them by Johnston and Levine (49) as shown in Table 4.

Table 4. Differential varieties of wheat (checks ) and their reaction to the physiologic races used.


Plants in each pot were classified as resistant, segregating, or susceptible, and plants in segregating pots were counted and individually classified as to reaction type.

The total number of lines was tested only to race 15. After the classification, the number of lines wes reduced; about 25 lines homozygous resistant or homozygous susceptible to race 15 were selected, the number depending not only on reaction type but also on seed available for tests using the other three races.

## EXPERIMENTAL RESULTS

Reaction of F4 Progeny of Wichita $x$ Webster to Race 15

The Wichita parent was not tested because it has been demonstrated many times that is completely susceptible to all races of leaf rust for which it has been tested (21, 42, 66, 80). The Webster parent was characterized by its typical 0; reaction.

The typical readings for the F 4 lines were 0 ; and 4 for
homozygous lines. In segregating lines, the reaction types were only 4 and 0 ;. No intermediate types appeared in the progeny.

The lines showing reaction type 0 ; with one or two plants a 4 -type, and those having reaction type 4 and one or two plants with a zero response were considered as mixtures and classified as homozygous for their reaction.

The summary of results is as follows:
Total lines of the cross..... 214
Homozygous resistant.......... 50
" susceptible....... 40
Segregating......... 124

In segregating lines:
Resistant plants..... 1,966
Susceptible plants... 1,258
Total... 3,2रा
Although statistical analysis was not applied due to the fact that the whole population did not represent a random sample, the results show that Webster carries a single, completely dominant gene for resistance to race 15.

The results of the tests of the selected lines of the cross ( either homozygous resistant or homozygous susceptible to race 15), to races 5, 9, and 105 are presented in table 5.

Table 5. Lines of the cross Wichita $x$ Webster selected for resistance or susceptibility to race 15 and their response to races 5,9 , and 105 .
Iine No. : race 15: race 5: race 9: race 105

| $\begin{array}{r} 12323 \\ 35 \\ 39 \\ 43 \\ 12346 \end{array}$ | $\begin{aligned} & 4 \\ & 4 \\ & 0 ; \\ & 4 \\ & 0 ; \end{aligned}$ | $\begin{aligned} & 4 \\ & 4 \\ & 0 ; \\ & 4 \\ & 0 ; \end{aligned}$ | $\begin{gathered} 4 \\ 4, \begin{array}{l} 4 \\ 4 \\ 4 \\ 4 \end{array}=3 \\ 27=4,5=3 \end{gathered}$ | $\begin{gathered} 4 \\ 4 \\ 4 \\ 4 \\ 1=4, \quad 4=2 \\ 19=3, \quad 1=1 \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: |
| 49 | 4 |  |  |  |
| 50 | O; | $0 ;$ | $33=4 ; 4$ | 4 |
| 55 | 4 | 4 | 4 | 4 |
| 57 58 | 4 | 4 | 4 | 4 |
| 62 | 4 | 4 | 4 | $19=4,4=0$ |
| 70 | 4 | 4 | 4 | - 4 |
| 72 | 0 ; | 0 ; | 4 | $7=4,3=2 t$ |
| 75 | 4 | 4 | 4 | $9=3$ |
| 77 | $0 ;$ | 0; | 4 | 4 |
| 83 | $0 ;$ | $0 ;$ | 4 | $12=4,3=24$ |
| 87 | 4 | 4 | 4 | $1=34$ |
| 91 | 4 | 4 | 4 | 4 |
| 95 | $0 ;$ | 0; | 4 | 4 |
| 96 | 4 | 4 | 4 | $8=4,3=0 ;$ |
| 98 98 | 4 | 4 | 4 | 4 |
| 99 12400 | 4 | 4 | 4 | 4 |
|  | $0 ;$ | 0 ; | 4 | $3{ }_{4}^{3+}$ |
|  | 4. | 4. | 3, 4 | 1 4 |
| 7 | 0 ; | 0; | 4 | $8=4 ; 7=3$ |
| 11 | 0 ; | 0 ; | 4 | $7=2 \nmid t, 1=4$ |
| 14 | 4 | 4 | 4 | 4 , |
| 17 | $0 ;$ | $0 ;$ | 4 | $\begin{aligned} & 6 \\ & 5\end{aligned}=2,6=3,200$ |
| 20 | 0 | 0 ; | 4 | $4=2,1=3,3=24$, |
| 26 | 0 ; | $0 ;$ | 4 | $21=4,5=1 \neq$, |
|  |  | $0 ;$ |  | 11=4, $7=3$ |
| 38 | $0 ;$ | 0 ; | 4 | $14=3-$, 14 $=2+t$ |
| 39 | $0 ;$ | 0 ; | 4 | $11=4,5=3$, |
| 54 | $0 ;$ | 0 ; | 4 | , $7=2 \mathrm{ft}$, |

Table 5. (Concl.)


Reaction of F4 Progeny of Wichita $x$ Webster to Race 5

The Wichita parent has a known 4-type reaction and Webster gave a 0 ; reaction.

The summary of results is as follows:
Total number of lines tested............. 57
Homozygous resistant. ................ 32
" susceptible............. 25

Intermediate or segregating lines were not found in the progeny and, as shown in table 5, the lines reacted in the same manner as to race 15 , with the only exception of line No. 12513, which may be mixture or just a misrecording. The conclusion is that a single completely dominant gene carried by Webster is responsible for the resistance to races 5 and 15 .

Reaction of P4 Progeny of Wichita $x$ Webster to Race 9
The Wichita parent has a known 4 -type reaction and Webster also gave a 4 -type reaction. As was expected, all the progeny appeared to be susceptible, and no transgressive segregation resulted. The off-types ( comprised between $2 f f$ and 3 ) were explained on the basis of rust-escaping plants.

Reaction of F4 Progeny of Wichita $x$ Webster to Race 105
The Wichita parent has a known 4-type reaction and Webster gave a $2 f f$ reaction.

The results are summarized as follows:
Total number of innes tested............. 56
Homozygous susceptible............. 29
Segregating. ........... . 27
Homozygous resistant............... 0
In segregating lines, plants reacted as follows:

| Reaction type | Number of plants |
| :---: | :---: |
| 0 | 24 |
| 1 | 1 |
| 1f | 8 |
| 2 | 10 |
| 24 | 26 |
| 2 ft | 59 |
| 3- | 16 |
| 3 | 166 |
| 4 | 188 |
|  | al 498 |

The number and nature of genes involved in the reaction of Wichita $x$ Webster to race 105 cannot be determined on the basis of these results, because they are rather inconsistent.

Reaction of F4 Progeny of Wichita x Carina to Race 15

The Wichita parent has a known 4 -type reaction and Carina a $0 ;$ reaction.

The results are summarized as follows:
Total lines of the cross....... 207
Homozygous resistant............. 49
" susceptible.......... 35
Segregating......... 123
In segregating lines, plants reacted as follows:

| Reaction type | Number of plants |
| :---: | :---: |
| 0; | 1,449 |
| $1-$ | 84 |
| 14 | 14 |
| 144 | 11 |
| $2-$ | 17 |
| 2 | 29 |
| 24 | 9 |
| 244 | 31 |
| 3 | 80 |
| 34 | 186 |
| $x(2 / 4)$ | 102 |
| 4 | Total |
|  | 2,931 |

The data suggest that there may be a single partially dominant gene carried by Carina responsible for resistance to race 15 .

The great range of reaction types shown by plants in the segregating lines of the cross is presumably due to environmental conditions. This abnormal behavior of Carine has been previously reported by Chester (8), Schulte (66), and Heyne and Johnston (21).

This erractic behavior may also be due to the presence of modifying genes or to a specific interaction between the host and pathogen, as shown by Heyne and Johnston (20) for Tlmstein, and by Harris (16) for Hussar.

The results of the tests of the selected lines of the cross ( either homozygous resistant or homozygous susceptible to race 15 ), to races 5, 9, and 105 are presented in Table 6.

Table 6. Lines of the cross Wichita $x$ Carina selected for resistance or susceptibility to race 15 and their resposse to races 5,9 , and 105 .
Line No. : race 15 : race 5 : race 9 : race 105


## Table 6. ( Cont. )

| Line No. | race 15 |  | race 5 | : race 9 | race 105 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| $\begin{aligned} & 75 \\ & 76 \\ & 78 \\ & 79 \\ & 87 \\ & 89 \\ & 93 \end{aligned}$ | 4 $0 ;$ $0 ;$ 4 $0 ;$ $0 ;$ $0 ;$ |  | $\begin{aligned} & 4 \\ & 0 ; \\ & 0 ; \\ & 4 \\ & 0 ; \\ & 0 ; \\ & 0 ; \end{aligned}$ | $16=3, \begin{gathered} 4 \\ 4 \\ 4 \\ 4 \\ 4 \\ 3 t \\ 4 \end{gathered}$ | $\begin{gathered} 4 \\ 4 \\ 4,4 p=3 \\ 4 \\ 4 \\ 22=4,7=3, \end{gathered}$ |
| $\begin{array}{r} 94 \\ 97 \\ 98 \\ 99 \\ 12703 \end{array}$ | $\begin{aligned} & 0 ; \\ & 0 ; \\ & 4 \\ & 4 \\ & 0 ; \end{aligned}$ |  | $\begin{aligned} & 0 ; \\ & 0 ; \\ & 4 \\ & 4 \\ & 0 ; \end{aligned}$ | $\begin{gathered} 24 t \\ 4 \\ 4 \\ 3,4 \\ 3=4,12=3, \end{gathered}$ | $\begin{array}{cl} 13=4, & 10=3 \\ 18=4, & 4=x \neq 6 \\ 18=4, & 5=x \neq 6 \\ 2=4, & 13=24, \end{array}$ |
| $\begin{array}{r} 8 \\ 10 \\ 11 \\ 21 \\ 34 \\ 37 \\ 46 \\ 47 \\ 53 \end{array}$ | $\begin{aligned} & 4 \\ & 4 \\ & 4 \\ & 4 \\ & 0 ; \\ & 4 \\ & 0 ; \\ & 0 ; \\ & 4 \end{aligned}$ |  | $\begin{aligned} & 4 \\ & 4 \\ & 4 \\ & 4 \\ & 0 ; \\ & 4 \\ & 0 ; \\ & 0 ; \\ & 4 \end{aligned}$ | $\begin{gathered} 4 \\ 4 \\ 14=4,4^{4} \\ 3=3 \\ 4 \\ 4,3 p=3 \\ 4 \\ 4 \end{gathered}$ | $\begin{gathered} 4 \\ 4 \\ 4 \\ 4=3 / 4,6 \mathrm{p}=x-6 \\ 4,3 \mathrm{p}=x 6 \\ 4,2 \mathrm{p}=x^{2} \end{gathered}$ |

Reaction of F4 Progeny of Wichita $x$ Carina to Race 5
The Wichita parent has a known 4-type reaction and Carina has a 0; reaction.

The results are as follows:

$$
\begin{array}{r}
\text { Total number of lines tested........ } 50 \\
\text { Homozygous resistant............ } 26 \\
\text { " } \\
26 \text { susceptiblo......... } 24
\end{array}
$$

As shown in Table 6, the reaction of the selected Ines of the cross was exactly the same as to race 15 , with the only exception of line No. 12628, which seems to be a mixture.

Therefore, the conclusion is that a single partially dominant gene carried by Carina apparently govern resistance to races 5 and 15 .

Reaction of F4 Progeny of Wichita $\times$ Carina to Race 9

The Wichita parent has a known 4-type reaction and Carina a reaction of 1-2.

The results are summarized as follows:
Total number of lines tested....... 52
Homozygous susceptible......... 27
Segregating......... 25
In segregating lines, plants reacted as follows:
Reaction type Number of plants

4
27


Reaction of F4 Progeny of Wichita x Carina to Race 105

The Wichita parent has a known 4 -type reaction and Carina a reaction of $1-2$.

The results may be summarized as follows:

$$
\text { Total number of lines tested....... } 50
$$

Homozygous susceptible........ 29
Segregating....... 21
In segregating lines, plants reacted as follows:
Reaction type Number of plants

| 0 | 1 |  |
| :--- | ---: | ---: |
| 2 | 5 |  |
| 24 | 13 |  |
| $24 f$ | 25 |  |
| $3-$ | 3 |  |
| 3 | 71 |  |
| 34 |  | 104 |
| 4 |  | 238 |
| $x$ |  | 22 |
|  | Total | 482 |

The same as to race 9, the resistance to race 105 contributed by Carina seems to be recessive in nature, but independently inherited.

Inheritance studies, as those reported in this thesis, represent one phase of an extensive program intended to the development of wheat varieties resistant to leaf rust.

The problem of breeding resistant varieties, as stated by Heyne and Johnston $(21,22)$ and Heyne $(80)$, is being attacked at the Kansas Agricultural Experiment Station by three different but interrelated methods: 1) conventional genetic studies, 2) monosomic analysis, and 3) transfer of the genes for resistance form the differential varieties to a common and stable genetic background.

The studies reported in this thesis correspond to the Pirst method, as well as inheritance of leaf rust reaction among the eight leaf rust differentials, as those reported by Mode (57) and Woodward (84).

The second method is based on the outstanding work on the aneuploids of common wheat made by Sears (67). The use of the 21 Chinese monosomics developed by Sears allowed Heyne and Livers (19) to determine the location of the gene for resistance to race 9 of Pawnee wheat on chromosome $X$.

The third method is being applied by the use of the backcross procedure. Pawnee winter wheat was selected as recurrent parent but it showed certain instability and has been replaced by Wichita, a stable susceptible variety.

As stated by Schulte (66), the objective of the backeross program through the information obtained from studies of the
inheritance of resistance may result in the production of a new Wichita, in which a great number of genes for resistance may be combined, if they are not allelic. In this manner, any mutation In the wheat plant or the appearance of other races not prevalent before in the area concerned might be unimportant.

The tests presented in this thesis were carried out in the seeding stage, a method suggested by several investigators, Newton and Johnson (58) among them. They have stated that seedling reaction is by no means reliable index to the leaf rust reaction of adult plants, at least when the seedilng reaction is of a susceptible type. On the other hand, when the seeding reaction is of a resistant type, it is a satisfactory guide to the reaction of the adult plant. It is evident that many wheat varieties that are susceptible in the seeding stage, become progressively less susceptible as they mature, Chinese spring wheat being a typical example.

Some apparent exceptions have been found: Harris (16) for example, reported that Carina and Brevit were resistant in the seedling stage to races 9 and 126 respectively, but susceptible In the adult stage. In most instances, however, the seeding reaction has proved to be valid.

The use of only four individual races in the experiments reported in this thesis, although it would appear as a rather limited number to draw valuable conclusions, is significant because, according to Chester ( 8 ) and more recently to Johnston (39) and Basile (2), each race studied represents a component of an important race group with an unified number. In this
manner, if a certain gene is found to govern resistance to one race, it can be assumed that it also is resistant to the other races in the group.

The fact that a gene may be responsible for resistance to many races at the same time is shown by Pawnee. This winter wheat originally was known to be resistant only to race 9, formerly the most prevalent race in Kensas. However, Pawnee has been found to be also resistant to races $10,11,13,19$, 20, 31, and 93 ( Table 1.).

The idea of breeding varieties resistant to only races prevalent in a given area, as proposed by Chester (8), is somewhat rejected by Schulte (66) because loss of resistance may occur due to a sudden or gradual change in prevalence of races caused by change in varieties. This case is also exemplified by Pawnee winter wheat in Kansas.

Sources of resistance, other than the differential varieties, are being sought and used in many parts of the world, as shown in Tables 1, 2, and 3, included in this thesis.

Cytogenetic studies, as those reported by Sears (68) are also being used as indirect tools for the solution of the problem of leaf rust of wheat. He was able to transfer the chromosome carrying the gene for resistance to leaf rust from Aegilops umbellulata to common wheat and later, using radiation, he transferred only the piece of chromosome carrying the gene for resistance.

All the concepts here discussed may be summerized by saying that the problem of breeding resistant varieties is being well
taken care of, and if the international cooperation now under way to the solution of the problem continues, permanent protection against this disease may be expected.

## SUMMARY

The seedling reaction to races 5, 9, 15, and 105 of leaf rust was studied in the F4 progeny of the crosses Wichita $x$ Webster and Wichita $x$ Carina.

Webster appeared to have a single, completely dominant gene for resistance to races 5 and 15 in the cross Wichita $x$ Webster.

No transgressive segregation was obtained in this cross when tested to race 9. All the progeny resulted susceptible, the same as the parents.

Inconclusive results were obtained testing the cross to race 105.

Carina appeared to have a single, partially dominant gene for resistance to races 5 and 15 in the cross Wichita $x$ Cerina.

The factors for resistance of Carina to races 9 and 105 appeared to respond in a recessive manner but were different for the two races.

The great variability in reaction obtained in the progeny of the cross Wichita $x$ Carina when tested with races 9,15 , and 105 is explained as due to environmental conditions, modifying genes, or specific interaction between host and pathogen.

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# AN ABSTRACT OF A THESIS 

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MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE COLIEGE
CF AGRICULIURE AND APPIIED SCIENCE

Leaf rust, Puccinia triticina Prikss., is one of the most severe diseases attacking wheat throughout the world, and the most destructive disease in Kansas.

The rust is composed of 163 physiologic races which are identifled on eight differential varieties.

The production of resistant varieties offers the most effective means of control, and at present there is a large number of resistant varieties available which are the result of breeding carried out in many parts of the world.

An extensive breeding program is being conducted at the Kansas Agricultural Experiment Station intended to the development of wheat varieties resistant to leaf rust. One of the methods being used is the transfer of the genes for resistance carried by the eight differential varieties into the winter wheats adapted to Kansas conditions.

Studies reported in this abstract comprise a part of one of the phases of that program.

The seedling reaction to races 5, 9, 15, and 105 of leaf rust was studied in the $\mathrm{P}_{4}$ progeny of the crosses Wichita $x$ Webster and Wiohita $x$ Carina. One race of rust was used at a time, taking care of cleaning the greenhouse section thoroughly before a new race was introduced. Ten days after planting, the plants were innoculated with the desired race by dusting them with urediospores of the pure culture of the rust propagated on a susceptible variety. Plants were maintained in a moist chamber for about 12 hours after innoculation, and the response was determined after approximately 10 days.

Classification of phenotypes was made according to the scale of response proposed by Mains and Jackson and later by Johnston and Mains. This scale goes from 0 (zero), which corresponds to the highest resistance, to 4 , the highest susceptibility, $X$ being an intermediate type in which more than one reaction type is found on the same leaf.

Wichita, the stable genetic background selected as recurrent parent in the backcross program, was not tested, because it has a known 4 -type reaction to all races. The reaction type of the other two parents corresponded to that given to thom in the International Register of physiologic races.

The results of the study showed that Webster appeared to have a single, completely dominant gene for resistance to races 5 and 15 in the cross Wichita $x$ Webster.

Testing the cross Wichita x Webster with race 9, all the progeny resulted susceptible, the same as the parents, and no transgressive segregation was obtained.

The nature of the response of Wichita $x$ Webster to race 105 could not be determined on the basis of the data obtained, because they were rather inconsistent.

Carina appeared to have a single, partially dominant gene For resistance to races 5 and 15 in the cross Wichita $\pi$ Carina.

The factors for resistance of Carina to races 9 and 105 appeared to respond in a recessive manner but were different for the two races.

The great variability in reaction obtained in the progeny of the cross Wichita $x$ Carina when tested with races 9,15 , and

105 wes explained as due to environmental conditions, the presence of modifying genes, or specific interaction between the host and pathogen.


[^0]:    Report of cooperative uniform cereal rust observation nurseries for the year 1951. U.S.D.A. Agr. Res. Ad. 33 (mimeographed), 1952.

