INHERITANCE OF RESISTANCE TO PHYSIOLOGIC RACES 15B (CULTURE TLM) AND 56 (CULTURE MBCT) OF STEM RUST (*PUCCINIA GRAMINIS* F. SP. *TRITICI*) IN SIX DURUM WHEAT (*TRITICUM DURUM* DESF.) CULTIVARS

By

EFREM BECHERE

Bachelor of Science
Addis Ababa University
Alemaya, Ethiopia
1977

Master of Science
Addis Ababa University
Alemaya, Ethiopia
1981

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of Oklahoma State University
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Thesis Approved:

Edward L. Smith
Thesis Adviser

Francis J. Gough

Owen D. Merkle

Robert L. Westerman

Norman N. Durham
Dean of the Graduate College

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CHAPTER I

INTRODUCTION

Stem rust, Puccinia graminis pers. f. sp. tritici Eriks. and E. Henn., continues to be a potential threat to the production of durum wheat (Triticum durum Desf.) as well as bread wheat (Triticum aestivum) in many parts of the world. It has long remained a problem which has stimulated intensive research on the wheat host plant, the pathogen, and their genetical relations.

According to Roelfs (59,60) and Luig (51), damage caused by wheat stem rust can be more spectacular than any other cereal disease. Millions of hectares of a healthy crop with high yield potential can be totally destroyed in a very short time. As an example, Roelfs (59) cites the epidemics of the 1940s and 1950s caused by races 56 and 15, respectively, in the United States, Canada, and Australia.

The pathogen has a high pathogenic variability, and physiologic races with new or genotypically widened virulence often arise. Hybridization, mutation, heterokaryosis and parasexualism are considered the chief means for the origin of new races (51, 60, 73). Thus, many physiological races and sub races have arisen which enable the fungus species to attack a wide range of host cultivars, although an individual race may possess only a narrow host range. Consequently, improved cultivars under cultivation often succumb to variant races or biotypes of the fungus and their useful life is greatly reduced. According to

Gough et al(18), resistant genes in these cultivars have, on the average, been rendered ineffective after about five years.

The use of resistant cultivars currently is the most economical and practical method of controlling stem rust of wheat. The ability to meet the threat of new rust races with resistant cultivars depends upon identifying new sources of genes for resistance and a thorough understanding of their mode of inheritance.

Major areas under durum wheat cultivation in Ethiopia are subject to severe depredations caused by frequent epidemics of stem rust. For many years, durum wheat has been the main type of wheat cultivated in Ethiopia. Assuming that co-evolution of new virulence patterns of the pathogen and host plants took place in isolation, it would be expected that prevalent physiological races would be more adapted to T. durum than to T. aestivum. Barberry (Berberis holstii) hosting the aecial stage of the fungus has been recorded only in a very few locations in Ethiopia. Since P. graminis f. sp. tritici occurs during the whole year in urediospore stage and the alternate host is not a significant reservoir for renewal of infection, the development of new races and biotypes probably evolve through mutations and parasexualism (1).

Although attempts have been made over the last thirty years to develop stem rust resistant cultivars of wheat in Ethiopia, the work on the genetics of rust resistance is of very recent origin. However, with the growing realization of the complex nature of the pathogen, particularly with regard to physiologic specialization, wheat breeders in the country are now concentrating upon the development of breeding techniques to face this challenge.

In Ethiopia where the pathogen persists in volunteer wheat plants as well as in out-of-season crops or grasses, it is essential that cultivars possess a durable type of resistance. As far as known, nothing has been published on the inheritance of stem rust resistance in the cultivars under investigation, which include Reichenbachii, Cocorit 71, Boohai, DZ04-118, and Marou (DZ04-688). These cultivars are commonly used as parents in the Ethiopian Wheat Breeding Program. The durum wheat cultivar Reichenbachii, in particular, is the most important source of stem rust resistance in Ethiopia and as such is being used extensively in breeding work. This cultivar, in the seedling as well as in adult plant stages, is resistant to most of the races of rust found in Ethiopia. Earlier works are related mostly to hexaploid wheats and relatively very few reports are available on durum (tetraploid) wheats.

The objective of this investigation is to study the inheritance of seedling resistance to two stem rust races - Race 15B (culture TLM) and Race 56 (culture MBCT) - in five durum wheat cultivars widely grown and extensively used in breeding programs in Ethiopia, and to identify within them the resistant genes of greatest value. It is hoped that an understanding of the mode of inheritance of reaction to stem rust will facilitate planning and successful implementation of breeding programs for the transfer of rust resistance.

CHAPTER II

LITERATURE REVIEW

Investigations on the reaction to physiological races 15B and 56 predominate in reported genetic studies of stem rust resistance. Heavy losses caused by races 15B and 56 necessitated an understanding of the inheritance of resistance to the two races, primarily to facilitate breeding programs. However, inheritance studies of genes for resistance to a few other races have been reported.

Seedling vs. Adult Plant Resistance

Goulden et al (21) studied the seedling and adult plant reactions of several common and durum wheat cultivars to sixteen physiological forms of P. graminis f.sp. tritici. A close correlation between seedling and adult plant reactions for all of the races was observed in 'Vernal', 'Khapli', and 'Iumillo'. However, 'Acme' and 'Pentad' exhibited a substantial level of mature plant resistance to the races to which they were susceptible as seedlings.

Depauw and Buchannon (10) compared the seedling and post seedling reactions of five cultivars of T. aestivum to eight races of P. graminis f. sp. tritici in field studies in Kenya. They reported that the seedling and post seedling reactions of 'Florence Aurore' were similar to the eight races. However, cultivars 'Hope', 'Africa Mayo', 'Kenya Page', and 'Conley' were susceptible as seedlings to several races, but

expressed a degree of resistance to these same races as post seedling plants.

Nazareno and Roelfs (54) reported a lack of correlation between seedling and adult plant resistances of 'Thatcher'. Sunderwirth and Roelfs (71) used 26 cultivars to study adult plant resistance conferred by Sr2 to races 15-TLM, 15-TNM, and 151-QSH. They reported that the resistance conditioned by Sr2 was non-race specific to the three races and was characterized by reductions in number, size, and pattern of uredia. The resistance was best expressed after anthesis. A reduction in uredial size usually was apparent on plants inoculated after the boot stage.

According to Dyck and Kerber (12), stem rust genes that confer moderate resistance in the seedling stage usually confer the same type of resistance in the adult stage.

Evans et al.(14) screened seedlings of 38 wheat cultivars with seven cultures of P. graminis f. sp. tritici prevalent in East Africa. They reported that except for two cultivars, adult plant reactions in field plots were positively correlated with seedling reactions.

Greenhouse vs. Field Studies

Early investigators confined their studies primarily to field reactions of naturally occurring inoculum rather than to specific races. Their main objective was the determination of dominance or recessiveness of resistance.

Hayes et al.(25) pointed out that the type of infection on seedlings in the greenhouse is not always the same as that which develops on the same cultivar in the field. It is difficult to make

studies of the reaction of cultivars to single rust races in the field because races other than the one in question may infect the plants. They stated that it is definitely known that cultivars and hybrids on which 0, 1, and 2 infection types (normally considered a resistant response) occur in the greenhouse also are resistant to the same forms of rust in the field. But, they said, it is also known that seedling plants apparently susceptible in the greenhouse are sometimes rather highly resistant in the field. According to them, this applies particularly to the 3, 4, and x infection types.

Clark and Smith (9) studied the segregation of 89 F_3 families of 'Nodak' x 'Kahla' for reaction to infection in the field. Their data showed that susceptibility was dominant to resistance. Biffen (6) had reported the same result as early as 1907.

Koo and Ausemus (46) suggested that field resistance of 'Thatcher' to a mixture of stem rust races was conditioned by 2 complementary, recessive, independent genes.

Knott and Anderson (42) reported that studies of adult plants in the field was less valuable than similar seedling studies for determining the genetics of resistance. In the field, factors such as diseases caused by other pathogens, moisture, weather and maturity influence the rust reaction of individual plants so that correct classification is often difficult or impossible. However, they suggested that field tests are desirable to compare seedling and mature plant reactions and to test for the presence of genes providing only mature plant resistance.

Backcross vs. F_2 Data

Knott and Anderson (42), suggested that analyzing segregating F_2 families derived from backcrosses to a susceptible variety has advantages over the study of F_2 lines. They stated that backcross ratios are simpler than those in directly descended F_2 generations and it is easier to separate genes for resistance and study their effects singly.

Inheritance Studies

Naming and Characterizing Resistance Genes

Ausemus et al. (4) suggested that genes for resistance to stem rust should be given the symbol Sr plus an arabic number to designate the locus. If the relationship of a new gene to those previously identified is not known, a subscript letter, preferably the first letter of the variety involved may be used temporarily. On this basis, about 37 genes have been given the symbol Sr plus arabic numbers.

Green et al.(22) produced backcross lines of the spring wheat 'Marquis' carrying resistance genes Sr6, Sr7, Sr8, Sr9, Sr10, and Sr6 plus Sr7. Then the reactions of these lines to 99 North American cultures of 29 races of stem rust and to 8 Australian cultures were determined. Genes Sr6, Sr8 and Sr9 conferred a uniform type of resistance to most of the cultures. Genes Sr7 and Sr10 conferred only moderate resistance to a few cultures. Genes Sr6, Sr8, and Sr9 appeared to confer the same kind of resistance in 'Marquis' after five backcrosses as in the source cultivars, but Sr7 and Sr10 seemed less

effective. Later, Sr11 was transferred to 'Marquis' by backcrossing (37).

Roelfs and McVey (61) tested a total of 72 to 120 wheat lines from 1970 through 1977 to characterize the reactions of various specific resistances to 100 to 300 cultures of P. graminis f. sp. tritici. They reported that the wheat genotypes could be classified into three groups based on their response to North American rust cultures : (i) those susceptible to all or nearly all of the cultures studied, i.e, Sr9f, 9g, 16, 18, 19, 20, 28, LC, McN, and Kt'2'; (ii) those differential in response, i.e, Sr5, 6, 7a, 7b, 8, 9a, 9b, 9d, 9e, 10, 11, 12, 14, 15, 17, 21, 23, Tt-3, dp-2, and X; and (iii) those "universally" resistant or nearly so, i.e, Sr13, 22, 24, 25, 26, 27, 29, 30, Tt-2, and Gt.

Seven genes conferring resistance to P. graminis f. sp. tritici in common wheat were identified by Knott (31,32,34) and Knott and Anderson (42). The genes were identified primarily by seedling reactions to single cultures of races 15B and 56 and were named according to the recommendations of Ausemus et al.(4) as Sr6 to Sr12.

Rajaram et al.(56) studied the genetics of resistance to stem rust in three common wheats, namely, 'Gamut', 'Timgalen' and 'W 3198'. 'Gamut' was found to possess the genes Sr6, Sr9b, Sr11 and one previously undescribed gene designated SrGt. 'Timgalen' was found to carry Sr5, Sr6, Sr8, SrTt, SrT. ' 3198' carried the genes Sr11, Sr13, and Sr17.

Inheritance of seedling resistance to stem rust in 'Webster' wheat (T. aestivum) was studied in test crosses and in crosses with the 'Chinese Spring' monosomics by Knott and McIntosh (43). The resistance of 'Webster' to several North American and Australian races of stem rust

was apparently due to a single gene located on the long arm of chromosome 5D. Since no previously designated gene for stem rust resistance in wheat has been located in chromosome 5D, the gene in 'Webster' has been designated Sr30.

The inheritance of rust resistance was studied in crosses between 61 selected T. aestivum lines and a susceptible parent (39). Resistance in most crosses was recessive and involved several genes that have small, probably cumulative effects, and act only in adult plants.

Crosses between cultivars of T. aestivum and varieties of T. durum and T. dicoccum were studied by Hayes et al. (24) in their investigation on genetics of rust resistance. Susceptibility was dominant in crosses between resistant durums and susceptible common wheats but recessive in crosses between resistant emmer and susceptible common wheats.

Inheritance of the three stem rust reactions, near immunity, resistance, and susceptibility, were studied by Clark and Humphrey (7), and Clark and Smith (8) in crosses involving 'Marquis' and 'Reliance'. Their result indicated that both cultivars had a dominant factor for susceptibility.

Results of studies conducted to determine the mode of inheritance of field resistance to stem rust in crosses of resistant 'N.P.790' with susceptible 'N.P.718', 'Pb.C.591', and 'Pb.C.281' were reported by Sikka and Rao (66). A mono-hybrid ratio of 3 resistant : 1 susceptible was observed in 'N.P.718' x 'N.P.790' while in 'Pb.C.281' x 'N.P.790' and 'Pb.C.591' x 'N.P.790' a tri-hybrid ratio of 61 susceptible : 3 resistant was observed. Resistance of 'N.P.790' was dominant in the cross with 'N.P.718' and recessive in the crosses with 'Pb.C.281' and 'Pb.C.591'.

Races 15B and 56

Recent studies have focused primarily on determining the genetics of resistance and the interrelation among the various genes in sources of resistance to the predominant races 56 and 15B. Knott and Anderson (42), Knott (31,32,35), and Knott and Shen (45) identified eight different gene loci that control reaction to these two races in approximately 30 cultivars. Other researchers have studied some of these cultivars and in most instances found the above genes did account for the resistance.

Kenaschuk et al. (29) determined the inheritance of reaction to race 15B in ten selections of durum wheat and identified four separate genes for rust resistance. Six of the selections, 'St.464', 'C.I.7805', 'P.I.192178', 'C.I.7870', 'C.I.7875' and 'C.I.8133', each carried resistance genes Srd2, and Srd5. Gene Srd4 was found to control resistance in 'Arabian', 'P.I.191449' and 'Golden Ball'. Resistance of 'Camadi' was controlled by Srd6.

Inheritance of reaction to race 15B in durum wheats 'Ld 357', 'Langdon' and 'C.I.3255', was investigated by Lund (53). His data indicated that seedling reaction to race 15B was governed by one major factor and two minor factors in the three cultivars.

In an attempt to locate new genes for stem rust resistance, Knott and Shen (45) studied 11 cultivars of common wheat of diverse origins. They backcrossed each cultivar to the susceptible parent 'Marquis' and tested the F_2 families from the backcross with races 15B and 56. Genes for resistance in each cultivar were identified from test crosses with cultivars carrying known genes and with lines of 'Marquis' carrying

single genes for resistance. They found that most of the resistance present in the 11 cultivars could be accounted for on the basis of known genes (Sr6 through Sr10). However, they identified at least one new gene which conditioned moderate resistance to race 15B, and possibly one or more new genes which conditioned moderate resistance to race 56.

Inheritance of resistance to race 15B and 56 of stem rust was studied by Knott (31) in 'Africa No. 43', 'Kenya C9906', 'Kenya 338. Ac.2.E.2', 'Egypt Na 101', 'Veadeiro' and 'P.I. 170910' (Red Egyptian type). Each cultivar was analyzed genetically in backcrosses to susceptible 'Marquis'. Interrelations of genes in the cultivars were determined from diallel crosses. Except for 'Veadeiro', all cultivars in the study carried various combinations of previously reported resistance genes. Resistance of 'Veadeiro' to race 15B was the mature plant type and appeared to be conditioned by two additive genes.

In a study on inheritance of resistance to stem rust races 15B-1 and 56 in 'French Peace' wheat, Knott (40) concluded that 'French Peace' probably carries resistance genes Sr7a, Sr9a, and Sr13.

Knott (37) studied the inheritance of resistance of 'H-44-24' to race 56, using F_2 families from a backcross to 'Marquis', and found that a single dominant gene controlled resistance. Probably, the same gene was present in 'Hope'. This gene was transferred to 'Marquis' and the symbol Sr1 was proposed for it.

Knott (38) studied the inheritance of resistance to race 56 and 15B-1L in a backcross of 'Hope' to 'Marquis' and demonstrated that resistance to race 56 was conditioned by two dominant genes (Sr1 which conditioned seedling resistance and Sr2 which conditioned adult plant resistance). A recessive gene controlled resistance to race 15B - 1L.

Both genes, Sr1 and Sr2, were required to provide full resistance to race 15B at either the seedling or adult plant stage. Green et al. (22), on the other hand, reported that genes Sr1 to Sr4 named by Ausemus et al. (4) confer adult plant resistance and cannot be studied effectively in seedling plants.

Knott and Anderson (42) found that 'Red Egyptian' carried three genes which conditioned seedling resistance to race 56 and 15B and assigned the symbols Sr6, Sr8, and Sr9.

In an attempt to locate more genes for stem rust resistance, Knott and Srivastava (44) backcrossed eight selections of stem rust resistant common wheats to susceptible 'Marquis' and 'Little Club' and studied their inheritance to races 15B and 56. The major genes carried by the selections, Sr8, Sr9, Sr7a, Sr9a or b, Sr9d, and Sr6 had all been identified previously.

Williams et al.(76) investigated the inheritance of resistance to eight cultures of stem rust in crosses between durum cultivars 'Ward' and 'Marrocos 9623'. They found that 'Ward' had two genes for resistance to two cultures of race 15 and one culture of race 15B.

Knott (41) reported that 'Marquillo' (Triticum aestivum) carried a single recessive gene for resistance to race 56 located on chromosome 3B. He identified the gene as Sr12 and pointed out that it appeared to be temperature sensitive.

Knott (36) studied the inheritance of several wheat cultivars to races 15 and 56. 'Thatcher' gave a variable reaction to race 56, presumably depending on the environmental conditions. 'H-44-24' had a single dominant gene conferring resistance to race 56. 'Marquillo' carried one recessive gene for moderate resistance to race 56. Data from

backcross of 'Khapstein' to 'Marquis' showed that it carried one gene for resistance to race 56 (35). The gene for resistance to race 15B proved to be Sr7. Of the two genes for resistance to race 56, one, Sr13 gave a type 2 reaction and the second, Sr14, produces a papery-grey necrosis around pustules of all sizes.

Knott and Anderson (42) reported that 'Kenya 58' carried two genes, Sr6 and Sr7, for resistance to race 15B. Gene Sr6 acted as a recessive gene and governed a high type of seedling resistance. Gene Sr7 was partially dominant for resistance and conditioned a moderately resistant reaction when in a homozygous condition. Aslam and Ausemus (2) also found that the resistance of 'Kenya 58' to race 11 was conditioned by two dominant genes. Later, Leisle and Ausemus (47) reported that 'N.S.II-50-17', a highly rust resistant wheat produced from 'Frontana' x 'Kenya 58'-'Newthatch', carried Sr6, Sr7, Sr8, and Sr9. The results confirmed that 'Kenya 58' carries Sr6 and Sr7, and that 'Frontana' carries Sr8 and Sr9, thus accounting for those genes in 'N.S.II-50-17'. Also, they reported a previously unknown dominant gene in 'Newthatch' which conditioned seedling resistance to race 56.

Sunderman and Ausemus (70), studied four hexaploid wheats and indicated that seedling resistance to race 15B was controlled by four genes. Two appeared to be in both 'Kenya 58' and 'Mayo 54' and were labelled genes D and E. Gene D was thought to be additive or partially dominant in action and resulted in a semi resistant reaction when present in the homozygous condition. Gene E acted as a recessive and governed high resistance.

Jones and Ausemus (28) used race 15B to test progeny of the cross 'Frontana' x ('Kenya 58' x 'Newthatch') and explained resistance on the basis of three independently inherited genes.

'Khapli' emmer has been a valuable source of stem rust resistance in many durum breeding programs. Numerous studies on the inheritance of 'Khapli's resistance to several races have been published. Heerman (26) concluded that two independent dominant genes in 'Khapli' conditioned seedling resistance to race 15B, and that four independent genes, two dominant and two recessive, conditioned adult plant resistance. Williams and Gough (74) reported that four genes in 'Khapli' conditioned seedling resistance to three races of stem rust. Three genes were tentatively identified as Sr7, Sr13, and Sr14. Gene Sr7 conditioned resistance to race 15B. Gene Sr13 imparted resistance to races 15B and 56, while Sr14 conditioned resistance to race 56 only. A fourth gene conditioned a slight degree of resistance to race 15B.

Knott (35) studied the genetics of rust resistance in 'Khapstein' to races 15B and 56. He studied crosses of 'Khapstein' with 'Marquis' and lines having Sr7, Sr9, and Sr11 in a genetic background of 'Marquis'. A two gene segregation (13:3) was observed for race 15B. One of the genes conditioning resistance to race 56 was reported to confer some resistance to race 15B also. He concluded that resistance of 'Khapstein' was governed by three genes, Sr7, Sr13, and Sr14.

Race 111

Race 111 has been used by several workers to study the genetics of stem rust resistance in durum wheat. Gough and Williams (20) reported that the resistance of each of the two durum cultivars 'Acme' and 'Mindum' to race 111 was governed by three independent, incompletely dominant genes.

Williams and Gough (75) investigated the inheritance of rust reaction of seven tetraploid wheat cultivars to stem rust culture 111-SS2. They reported that three dominant genes conditioned the resistance of 'Spelmar' and that any two of the three genes produced infection type 0;. Singly, two of the genes conditioned infection type ranging from 0; to 3-. A third gene conditioned necrosis around the pustules. Three independently inherited dominant genes governed the resistance of 'Camadi Abdu Tipo'. A three factor hypothesis was postulated for two other cultivars, 'St 464' and 'Iumillo'. There was lack of agreement between F_3 data of 'C.I.8155' x 'Marrocos 9623' and backcross data. Either two or three incompletely dominant genes were indicated for the resistance of 'C.I.8155'. Only one major gene was found to condition the resistance of 'Kubanka'. The data on 'Vernal' were inconclusive but indications of a three factor segregation were evident.

Genetic studies of standard stem rust differential tetraploid wheats indicated that 'Mindum', an 'Acme' selection, 'Spelmar', and 'Vernal' emmer each had three genes for resistance to the culture 111-SS2 of stem rust (20,75). 'Kubanka' had one gene for resistance to culture 111-SS2 (76), and 'Khapli' emmer had three genes for resistance to culture 111-SS2 (74).

Gough et al.(19) studied the resistance of the Russian wheat (T. aestivum) cultivar 'Skorospelka 3b' to culture 111-SS2 of P. graminis f.sp. tritici and found that it is conditioned by two dominant independent genes, tentatively designated SrSO1 and SrSO2.

Gough and Merkle (17) studied inheritance of seedling resistance to stem rust in T. aestivum 'C.I.14115' x susceptible 'Little club'. Resistance to culture 111-SS2 (physiological race 111) was conditioned by two independent dominant genes. Gough and Merkle (16) also studied inheritance of stem rust resistance in T. aestivum cultivars 'Agent' and 'Agrus' and concluded that both cultivars have at least four genes for resistance to culture 111-SS2 (race 111). The four genes were tentatively designated Ag-1, Ag-2, Ag-3, and Ag-4.

Loegering and Powers (48) studied the inheritance of pathogenicity in a cross between physiological races 111 and 36 of stem rust. They inoculated 'Marquis' with 108 F_2 cultures, and the results indicated segregation for two independently dominant genes for avirulence. They concluded that 'Marquis' had at least two genes for resistance to race 111.

Berg et al.(5) studied the inheritance of seedling resistance to a single spore culture of 111 - SS2 (race 111) in the F_1, F_2, F_3, and backcross F_1 from crosses of 'Marquis' with the susceptible cultivar 'Little Club' and concluded that at least three independent dominant genes conditioned the resistance of 'Marquis'. These genes were tentatively labelled Srmq1, Srmq2, and Srmq3.

Rondon et al. (62) reported that seedling resistance to physiologic race 111 (culture 111-SS2) of P. graminis f. sp. tritici was conditioned

by two and three independent genes, respectively, in the durum wheat 'P.I. 94701' and the common wheat 'Reliance'.

Riede et al. (58) crossed 'Estanzuela Dakuru' with susceptible 'Little Club' and investigated the inheritance of seedling reaction in the greenhouse to culture 111-SS2. The result indicated that 'E. Dakuru' had four dominant genes, SrDS2, SrDS3, and SrDS4 for resistance to culture 111-SS2.

Other Races

Smith (67) determined the genetics of stem rust reaction to races 17 and 147 in a cross of 'Mindum' durum and 'Vernal' emmer. He found that adult plant reaction to natural infection in the field and seedling reaction to race 17 were correlated. Data from tests with both races 17 and 47 fit a ratio of 1 homozygous resistant : 2 segregating : 1 homozygous susceptible. Tests of the same lines with race 147 revealed that progenies homozygous for resistance to race 17 were homozygous for susceptibility to race 147, and those homozygous for susceptibility to race 17 were homozygous for resistance to race 147. Lines homozygous for susceptibility or resistance to both races were not discovered.

Inheritance of seedling resistance to races 17, 21, 29, and 36 in a cross of 'Vernal' x 'Marquis', as reported by Harrington and Smith (23), was governed by a single dominant factor designated Rb which also controlled the reaction to races 17, 29, and 36.

Rust resistance of 'Marquis' in the seedling stage was conditioned by a single dominant gene when tested with race 19 (55). Harrington and Smith (23) reported that seedling resistance of 'Marquis' to race 27 was conditioned by a single gene.

Jones and Ausemus (28) used races 11 and 38 to test progeny of 'Frontana' X ('Kenya 58' X 'Newthatch'). Both parents and all progenies were resistant to race 38.

Riede et al.(58) studied the inheritance of seedling reaction to cultures GB 121 and 72 of P. graminis Pers. f. sp. tritici in crosses of T. aestivum 'Estanzuela Dakuru' with susceptible 'Little Club' and 'BH 1146'. Their tests indicated that 'E. Dakuru' had three genes (SrDG1, SrDG2, and SrDG3) for resistance to GB 121 and one for resistance to culture 72.

To study the inheritance of stem rust resistance in 'Tobari' and 'Zambesi', Jain and Gandhi (27) analyzed data from F_1, F_2, F_3 and backcross F_2 seedlings tested with stem rust races 21 and 40. They found that genes Sr8 and Sr11 protected both cultivars against races 21 and 40 and that gene Sr5 in 'Tobari' was effective against race 21 only.

William et al. (76) studied the inheritance of resistance to stem rust in crosses between a resistant durum cultivar, 'Ward', and a susceptible durum cultivar, 'Marrocos 9623'. Resistance to culture of race 121 was probably conditioned by two genes. 'Ward' had three genes for resistance to cultures of races 9, 11, and 29.

Ataullah (3) reported that two independent dominant genes in 'Khapli' controlled resistance to races 21-2 and 222-4. One of the two genes was effective also against race 126.

Gene Interactions, Allelism, Linkage and Background Effects

Different types of interactions between stem rust resistant genes have been discussed (5,12,20). It has been suggested that a cultivar

with two genes, each determining a different level of resistance, usually exhibits the rust reaction phenotypic of the most effective gene; the gene conferring the least resistance is masked. The most effective gene is epistatic to those that condition a less resistant reaction. Furthermore, a cultivar with two or more genes is presumed to be resistant to all of the rust races to which the genes are effective separately. However, genes for disease resistance do not invariably act independently. The gene action may be complementary, that is, genes at different loci or their products may interact to give higher levels of resistance. Host plants with either gene alone can be susceptible while plants with both genes are resistant. This type of complementary action, they indicated, has usually been exhibited between recessive genes.

There are examples of genes for disease resistance that interact to give an enhanced level of resistance (42,64). This complementary interaction, which may be additive, results in a higher level of resistance than that conferred by the genes singly. Dyck (11) found that 'P.I.58548' has two genes for seedling resistance to leaf rust, one giving a 1+ infection type and the second a 2+. When combined the two genes interact to produce ; to 1 infection types. More recent studies (13,63) have shown additional interactions between each of two different pairs of genes conditioning seedling resistance, between a pair conditioning adult plant resistance, and between a pair conditioning seedling and adult plant resistance. But Dyck and Kerber (12) warn that not all genes that result in intermediate levels of resistance will, when in combinations with other genes, interact to give superior resistance.

From their studies in the inheritance of seedling resistance to a single spore culture of 111-SS2 (race 111) in the F_1, F_2, F_3, and backcross F_1 from crosses of 'Marquis' with susceptible 'Little Club', Berg et al. (5) concluded that at least three independent dominant genes conditioned the resistance of 'Marquis'. They indicated that two of these genes were cumulative in effect and that they were epistatic to the third gene.

Aslam and Ausemus (2) found that the resistance of 'Kenya 58' to race 15B was governed by two independently inherited genes with an additive effect.

The mode of inheritance of seedling resistance for six stem rust races (P. graminis f.sp. tritici) was studied by Raut et al.(57) in five crosses involving tetraploid wheat cultivars. Their findings revealed that seedling resistance was due to mono-, di- or tri-genic factors involving duplicate and complementary gene interactions.

There are also examples of nonallelic additive interactions, in stem rust of wheat. Knott (32) noted that resistance genes Sr10, Sr11, Sr12 and particularly Sr9 were important modifiers of gene Sr7. Luig and Rajaram (52) studied the stem rust reaction of homozygous and heterozygous combinations of Sr5 and Sr9b, Sr5 and Sr13, Sr6 and Sr8, and Sr8 and Sr9b. Additive gene interactions were observed especially when Sr6 was involved. It would appear that some genes are more sensitive to nonallelic interaction than others.

The importance of modifiers on rust resistance is emphasized in Knott's work (31). In 'Kenya 338.AC.2.E.2' he reported that there was one main modifier of Sr7 which conditioned resistance to race 15B. Evidence presented by Knott and Anderson (42) indicated that in 'Kenya

117A' and 'Egypt Na95' either Sr9 or Sr10 or both acted as modifiers of the gene Sr7. This "modifier effect" probably explains many of the difficulties encountered in maintaining full resistance while back crossing to produce rust resistant cultivars.

Knott and Anderson (42) found that genes which by themselves provided resistance only to race 56 acted as modifiers of resistance to race 15B. They pointed out that two cases of a single gene giving resistance to both races had been found. This, they said, suggests that resistances to races 15B and 56 are closely related physiologically.

Genes conditioning host resistance can also be inhibited or suppressed by nonallelic genes. Kerber and Green (30) observed that 'Canthatch nullisomic 7D' was much more resistant to several cultures of stem rust than normal disomic 'Canthatch'. They concluded that chromosome 7DL carries a gene that inhibits the expression of one or more genes for rust resistance present on other chromosomes of 'Canthatch'.

Genetic background can also affect the expression of specific genes for resistance. A gene for resistance may be dominant in one genetic background and recessive in another. Consequently, the susceptible parent in a cross may influence the degree of dominance of a gene (12).

The reaction conferred by a gene may be dominant relative to one race of the pathogen and recessive to another (42). It has been suggested that this phenomenon may be due to two closely linked genes, in which the expression of one is dominant and the other recessive. Knott and Srivastava (44) presented data supporting this suggestion. They reported that gene Sr6 was often completely dominant to race 56 but recessive to race 15B in 'Marquis' backcross lines. However, with

'Little Club' backcross lines, Sr6 behaved as a dominant gene to both races.

Nullisomic analysis of stem rust resistance in T. vulgare var. 'Timstein' by Sears and Rodenhiser (65) indicated that 'Timstein' was resistant to race 56. When F_2 populations from crosses of 'Chinese Spring' nullisomics with 'Timstein' were tested, all but one showed the expected segregation pattern of 9 resistant : 7 susceptible. From these results, they concluded that 'Timstein' carried two dominant complementary genes for resistance to race 56. These genes were located on chromosome X.

When two or more genes are on the same chromosome, they may show varying degrees of linkage. In some cases the genes are either tightly linked or they are allelic, that is, they are at the same locus on a chromosome. Such tight linkage, or multiple allelism may restrict the number of genes that can be combined into one cultivar. Allelism, together with a scarcity of resistant genes, has been a particular problem in the development of stem rust resistant cultivars. Convincing proof of whether two or more resistant cultivars have the same (allelic) or different (non-allelic) genes for resistance can be obtained only by genetic tests of appropriate hybrids.

Evidence of allelism for resistance to wheat stem rust was first reported by Smith (67) in 1957. He determined the genetics of stem rust reaction to races 17 and 147 in a cross of 'Mindum' durum and 'Vernal' emmer. His data indicated that each parent carried one pair of genes for resistance and that the two genes were allelic or closely linked. Green et al. (22) found that genes for resistance at the Sr9 locus in 'Red Egyptian' (Sr9a) and 'Kenya 117A' (Sr9b) were allelic. Loegering and

Sears (49) demonstrated that this suggestion was valid. Later, Knott and Srivastava (44) pointed out that six alleles for resistance are known at the Sr9 locus. Loegering and Sears (50) reported two alleles for resistance at the Sr7 locus, Sr7a in 'Kenya Farmer' and Sr7b in 'Hope' and 'Sapporo'.

Ghosh et al. (15) studied the inheritance of resistance to stem rust in four crosses of T. aestivum and concluded that mature plant resistance was inherited in a 13 (susceptible) : 3 (resistant) ratio in the cross 'N.P. 790' (resistant) x 'N.P. 775' (susceptible). This ratio indicated dominant and recessive gene interaction. A dominant gene at one locus (A) and a recessive genotype (bb) at the other locus produced the same phenotype.

CHAPTER III

MATERIALS AND METHODS

Five crosses within T. durum in which 'Reichenbachii' was the common stem rust resistant parent, were studied in the F_1, F_2 and backcross F_1 to determine the mode of inheritance of seedling reaction to cultures TLM (race 15B) and MBCT (race 56) of P. graminis f.sp. tritici. The study was conducted in a greenhouse and a growth chamber at Oklahoma State University, Stillwater, commencing in the fall of 1984 and extending through the spring of 1987.

Durum Wheat Genotypes

The six durum wheat cultivars studied and their reactions to cultures TLM and MBCT are presented in Table I. A brief description, the pedigree as known, and the origin of each cultivar is given below :-

'Reichenbachii' - The source of this cultivar is not known with certainty. According to D. H. Smith Jr. (personal communication, 1987), the cultivar was introduced into the United States National Small Grains Collection by N. I. Vavilov from Leningrad in 1924. CIMMYT workers (personal communication, 1986) indicated that it was an introduction from India. It is a tall, late maturing cultivar having red seed, a high level of resistance to most stem rust races, and generally poor agronomic characteristics in Ethiopia. It is presently being used in the Ethiopian durum improvement program as a source of stem rust resistance.

'Cocorit 71' - An early maturing selection made at CIMMYT from Rae/4*Tc60//Stw63/3/AA"S"D27617-18M-67-0m. It was released in Ethiopia in 1976. It is awned, with white chaff and amber grains. It is a short stature cultivar with two dwarfing genes (72).

'Boohai' - An early maturing selection made at Debre Zest, Ethiopia, from an F_2 bulk population of a complex cross Cr "s" (21563/61-130 X Lds) Candeal II, CD38862 obtained from CIMMYT in 1974. It is tall, awned, and possesses white chaff with amber grain (72).

'Marou' (DZ04-688) - A late maturing selection from a local land race in Ethiopia. It has amber seed and white chaff and large spikelets. It has low level of resistance to stem rust.

'DZ04-118' - A medium maturing selection from a local land race in Ethiopia. It has pubescent spikes, white chaff and amber seed color. It is generally susceptible to stem rust and has a tendency to lodge

'Marrocos 9623' (P.I.192334) - A late maturing Portuguese cultivar (20) which is susceptible to most stem rust races. It is tall with big, very compact, club-shaped heads and has black, very rough awns.

'Reichenbachii', 'Cocorit 71', 'Boohai', 'Marou' (DZ04-688), and 'DZ04-118' were obtained from Debre Zest Agricultural Experiment Station, Ethiopia. 'Marrocos 9623' was obtained from the Department of Plant Pathology, Oklahoma State University.

All cultivars were crossed with the stem rust resistant parent 'Reichenbachii'. The F_1 from each cross was backcrossed to the relatively more susceptible parent and the populations in Table II were produced.

A set of differentials for the two races used in the investigation were planted along with the other materials to assure that the two

cultures truly represented races 15B and 56, and also to assure that no cross contamination occurred between the two cultures during the course of the study. These genotypes, which were obtained from the Cereal Rust Laboratory at St. Paul, Minnesota, are listed in Table III with their reactions to races 15B (culture TLM) and 56 (culture MBCT).

TABLE I

CULTIVARS USED IN THE STUDY, THEIR ORIGIN AND REACTIONS TO CULTURES TLM (RACE 15B) AND MBCT (RACE 56) OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

Cultivar	Origin	Rxn.to race 15B(TLM)[a]	Rxn.to race 56(MBCT)[a]
Cocorit 71	CIMMYT	;	$0;1^{-}$
Boohai	CIMMYT	$X(;,1,2,3^{=})$	0;1
Reichenbachii	India	0	0
DZ04-118	Ethiopia	4	$2^{-},2$
Marou	Ethiopia	$;,1^{-}$	$0;13^{=}$
Marrocos 9623	Portugal	4	4

[a] Rxn. = infection types on seedling leaves of indicated cultivars.

TABLE II

NUMBERS OF F_1, F_2, AND BACKCROSS PLANTS TESTED IN THE STUDY

Crosses	No. of F_1 plants tested with		No. of backcross plants tested with		No. of F_2 plants tested with	
	TLM	MBCT	TLM	MBCT	TLM	MBCT
Cocorit 71/Reichenbachii	4	5			402	503
Reichenbachii/Cocorit 71		5				514
Coc. 71/Reich.//Coc. 71			87	80		
Boohai/Reichenbachii	4	4			398	408
Reichenbachii/Boohai		5				503
Boohai/Reich.//Boohai			81	88		
Marou/Reichenbachii	4	5			407	509
Reichenbachii/Marou		5				513
Marou/Reich.//Marou			97	89		
DZ04-118/Reichenbachii	4	4			359	408
Reichenbachii/DZ04-118		5				518
DZ04-118/Reich.//DZ04-118			65			
Marrocos 9623/Reich.	4	4			293	369
Reich./Marrocos 9623	4	4			338	373
Marrocos 9623/Reich.// Marrocos 9623			85	80		

TABLE III

SET OF DIFFERENTIALS USED TO DIFFERENTIATE BETWEEN RACES 15B AND 56 OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

Differentials (cultivars or lines)	Resistant genes in the differentials	Infection types with race 15B	race 56
1. Carlton (DW)	Sr 9e	4	;1
2. Medea Ap 9d (DW)	dp-2	2	2-
3. DA-3 (DW)	Sr 9e	4	1
4. Isr 11 Ra (BW)	Sr 11	4	1-
5. Bt Sr 12 Tc (BW)	Sr 12	4	0;
6. St 464 Sr 13 (DW)	Sr 13	2	2
7. Line A (BW)	Sr 14	4	2CN[a]
8. H-1 (BW)	Sr 7a	4	1CN[a]
9. Pd/8*Mg/2*EspJ/8/9(BW)	Sr 17	0;	4
10. Vernal (emmer)	Sr 9e	4+	1=
11. BL 116-A5 (DW)	?	4	1⁻

[a] C and N refer to chlorosis and necrosis, respectively.

Source of Innoculum

Initially, single spore cultures of races 15B and 56 were obtained from Dr A. Roelfs, Minnesota Rust Laboratory, ARS, St. Paul, Minnesota. The cultures were designated as TLM and MBCT and identified as physiological races 15B and 56, respectively, using the stem rust differentials in Table II. Innocula of the cultures were multiplied on the highly susceptible wheat cultivars 'McNair 701' and 'Little Club' under isolation in growth chambers at Stillwater and then stored in sealed glass tubes under liquid nitrogen until used.

There was a widespread appearance of race 15B of stem rust in 1950 in the United States. All commercial bread and durum cultivars of spring wheat resistant to previously predominant races were heavily attacked. Race 15B has continued to be a principal obstacle to the production of resistant cultivars of wheat (33,68). Races 15B and 56 were originally collected in the U.S.A. in 1917 and 1928, respectively, and identified by staff at the University of Minnesota. Race 15B is a widely virulent race. Even though race 56 is not as widely virulent as race 15B, it still is a prevalent race (34).

Race 15 is prevalent in the stem rust population in Ethiopia. It was also ascertained that race 15B was present in the population because the wheat 'Lee', which is a differential variety used to distinguish between races 15B and 15, was susceptible.

Moreover, races 15B and 56 will detect almost all resistance genes identified in durums. Therefore, use of these two different races should permit detection of new and useful genes for stem rust resistance.

Planting and Innoculation

Ten plants of each of the parent and differentials and four F_1 plants from each cross were included in all tests. Two separate growth chambers were used throughout the study to avoid cross contamination of the rust spores. The plants were inoculated at the one to two leaf stages. Seedling leaves were first rubbed with moistened fingers to remove the waxy cutin and then dusted with a mixture of talcum (10 ml) and uredospores (0.5 ml).

After inoculation the plants were enclosed in a plastic tent for 24 hr. at approximately 100% relative humidity at about 22°C of temperature. At the end of 24 hr., the inoculated seedlings were subjected to slow drying for 2 hr. and incubated for 12 to 15 days at 22 to 25°C. During the incubation period, supplemental light was provided using high intensity cool white fluorescent lamps.

Data Collection

After 12 to 15 days of incubation, single leaves from individual plants were detached, labelled, and grouped according to infection type. Infection types of the groups were described in accordance with the system proposed by Stakman et al. (69). Infection types with corresponding symptoms are shown in Table IV. In this system, seedlings with infection types 0, ;, 1, 2, and 3 were considered resistant and those with infection type 4 were considered susceptible. Plus and minus signs were used to indicate variation within infection types. Thus, 3^- was used to indicate that the infection type fell in the 3 class but was close to class 2, while a 3^+ was used to indicate that the infection

type was near the upper limit of the 3 class. The letters C and N were used to indicate chlorosis or necrosis, respectively. A comma was used to separate discrete infection types on a single leaf and two infection types written together (for example, 23 or 0;) was used to indicate continued variation between the two types on a single leaf. The infection types were written in decreasing order of frequency. Plants with mesothetic reaction were recorded as X.

Analysis of Data

Data from F_2 plants and reciprocals as well as backcross F_1 plants were analyzed from each cross. To compare the observed and expected genetic ratios on the basis of Mendelian segregation, the chi-square test for goodness of fit was used. Data from F_2 population derived from different F_1 plants were tested for heterogeneity by chi-square and pooled when homogeneous.

TABLE IV

DESCRIPTION OF INFECTION TYPES USED IN THE STUDY[a]

Infection types[b]	Symptoms
0	No uredia or sign of infection.
;	No uredia. Necrotic or chlorotic flecks.
1	Small uredia surrounded by chlorosis or necrosis.
2	Small to medium uredia surrounded by chlorosis or necrosis.
X	Variable size uredia on a single leaf.
3	Medium-sized uredia associated with chlorosis or rarely necrosis.
4	Large uredia without chlorosis or necrosis.

[a]After Roelfs and McVey (61); Stakman et al.(69)
[b]Can be modified by using + and - signs.

CHAPTER IV

RESULTS AND DISCUSSION

Culture TLM (race 15B)

DZ04-118/Reichenbachii

Infection types of the parental, F_1, F_2, and backcross F_1 generations are given in Table V. The 359 F_2 plants tested with culture TLM (Race 15B) were derived from four F_1 plants. A Chi-square test for heterogeneity indicated that the data from the different families were homogeneous (P between .70 and .80) so the data were combined. Based on infection types, the plants were separated into four phenotypic classes in an observed ratio of 190 with infection type 4 : 74 with infection types 2 to 3^+ : 73 with infection types ; to 1^+ : 22 with infection type 0. The observed distribution was an acceptable fit to a 9:3:3:1 ratio (P between .50 and .70). The progenies of F_2 plants with infection types 0 and 4 (both parental types) were kept separate, whereas infection types ; to 1^+ were combined into one class and 2 to 3^+ into the other class for the chi-square analysis. This ratio indicates that Reichenbachii has two independent recessive genes for resistance to culture TLM (Race 15B). Knott (41) and Clark and Smith (9) also indicated that resistance was controlled by recessive genes in their inheritance studies on stem rust. Singly, one of the genes from Reichenbachii conditioned infection types ; to 1^+ and the second gene

conditioned infection types 2 to 3^+. Apparently, the two genes in combination interacted to condition infection type 0. In the absence of both genes, infection type 4 was observed. Both Dyck and Kerber (12) and Dyck and Samborski (13) have given examples of genes for rust resistance that interact to give an enhanced level of resistance. According to them, this complementary interaction , which may be additive, results in a higher level of resistance than that conferred by each gene singly. They further indicated that this type of complementary action has usually been between recessive genes.

The infection type on the F_1 plants were similar to the infection type on DZ04-118 (infection type 4) thus indicating the dominance of susceptibility over resistance in this cross.

The population of 65 backcross F_1 seedlings of DZ04-118/Reichenbachii//DZ04-118 all had infection type 4, thus supporting the two recessive gene hypothesis from the F_2 data. This result also confirmed the dominance of susceptibility.

The proposed genotypes for the F_2 and backcross F_1 are given in the Appendix (Tables XIV and XV). The effect of the two recessive resistant genes from Reichenbachii is masked in the heterozygote condition in the F_1. Hence, the F_1 was completely susceptible. The backcrossed material was again susceptible because the recessive resistant genes aabb from Reichenbachii were not present, i.e., all were dominant AABB, or they were at heterozygous loci A-B- and therefore ineffective.

TABLE V

SEEDLING REACTIONS OF PARENTS, F_1, F_2 AND BACKCROSS F_1 PLANTS FROM DZ04-118/REICHENBACHII TO CULTURE TLM OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

Parents or hybrids	Infection types				Total plants
	0	;to1+	2to3+	4	
Reichenbachii	10				10
DZ04-118				10	10
F_1				4	4
F_1 (reciprocal)				4	4
F_2 (observed)	22	73	74	190	359
Ratio (expected)	1	3	3	9	
Expectation	22.4	67.3	67.3	201.9	359
Backcross F_1				65	65

$X^2 = 1.8583$
$.50 < P < .70$

Marrocos 9623/Reichenbachii

Data for Marrocos 9623/Reichenbachii are presented in Table VI. The F_2 of Marrocos 9623/Reichenbachii consisted of 293 plants derived from two F_1 plants. The F_2 plants segregated into four phenotypic groups: 16 were classified as immune as Reichenbachii (0 infection type), 46 highly resistant (; to 1^+ infection types), 59 as moderately resistant (2 to 3^+ infection types) and 172 as susceptible (4 to 4^+ infection types). The chi-square test for heterogeneity indicated that the combined data from the two F_2 families fit a 9:3:3:1 ratio (P between .50 and .70) and that the families were homogeneous (P between .80 and .90).

Eighty-five backcross F_1 plants from Marrocos 9623/ Reichenbachii//Marrocos 9623 were also tested with culture TLM and all backcross F_1 plants developed infection types 4 to 4^+ (similar to the F_1 reaction). These responses coupled with those of the F_2, indicate that susceptibility is dominant to resistance. These results conform to those obtained from DZ04-118/ Reichenbachii in that resistance to culture TLM (race 15B) in Reichenbachii is controlled by two independent recessive genes. One of the genes, arbitrarily designated as aa, conditions infection types ; to 1^+, and the other gene bb, conditions infection types 2 to 3^+.

Again, it was observed that these genes interacted cumulatively to condition a higher level of resistance (0 infection type) than that conditioned by each gene singly. The 4^+ infection type is attributed here to environmental effects.

The reciprocal cross, Reichenbachii/Marrocos 9623, was also tested with culture TLM. The F_2 populations derived from three F_1 plants were

tested and the combined populations segregated into 19 (infection type 0), 64 (infection types ; to 1^+), 62 (infection types 2 to 3^+) and 193 (infection types 4 to 4^+). The populations were homogeneous (P between 0.80 and 0.95) and the data were combined. The chi-square value (0.2898) indicated that the observed numbers were a good fit to a ratio of 9:3:3:1 (P between 0.95 and 0.99). Susceptibility, in the reciprocal cross was dominant. These data further confirm the hypothesis of two independent recessive resistant genes in the cultivar Reichenbachii.

No difference was observed between the F_2 and its reciprocal. The chi-square for heterogeneity between the two F_2 populations and the three reciprocal F_2 populations indicated that they were homogeneous ($P > 0.95$) The data from these populations were therefore pooled to test a fit to a 9:3:3:1 digenic ratio. The chi-square value for the pooled data (1.4311 with P value between 0.50 and 0.70) again confirmed that the data are a good fit to the proposed ratio. It could also be inferred from the available data that maternal effects have little or no impact on inheritance of the resistance.

The proposed genotypes for the F_2, its reciprocal, and backcross F_1 are given in the Appendix (Tables XVI and XVII). As expected from the hypothesis that Reichenbachii has two recessive resistant genes, the F_1 and backcross materials were all highly susceptible. This again is explained by the fact that the effect from both recessive genes is not expressed in the heterozygous condition.

TABLE VI

SEEDLING REACTIONS OF PARENTS, F_1, F_2, RECIPROCALS AND BACKCROSS F_1 PLANTS FROM MARROCOS 9623/REICHENBACHII TO CULTURE TLM OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

Parents or hybrids	Infection types				Total plants	X^2	P Value
	0	;to1+	2to3+	4to4+			
Reichenbachii	10				10		
Marrocos 9623				10	10		
F_1				2	2		
F_1(recip.)				3	3		
F_2	16	46	59	172	293	2.3499	.50-.70
Ratio	1	3	3	9			
Expectation	18.3	54.9	54.9	164.8	293		
F_2(recip.)	19	64	62	193	338	0.2898	.95-.99
Ratio	1	3	3	9			
Expectation	21.1	63.4	63.4	190.1	338		
F_2 and recip. (pooled)	35	110	121	365	631	1.4311	.50-.70
Ratio	1	3	3	9			
Expectation	39.4	118.3	118.3	354.9	631		
Backcross F_1				85	85		

Marou/Reichenbachii

The 407 F_2 plants derived from four F_1 plants of Marou/Reichenbachii segregated for resistance and susceptibility to culture TLM (race 15B) in a ratio of 22 similar to Reichenbachii (0 infection type), 299 similar to Marou (; to 1^+ infection types), 23 intermediate to Marou and susceptible (2 to 2^+ infection types) and 63 susceptible (4 infection type).

All 97 backcross F_1 plants of Marou/Reichenbachii// Marou had infection types similar to Marou (; to 1^+) (Table VII). The chi-square test for heterogeneity indicated that the four F_2 families were homogeneous (P value > 0.99). Consequently, the data from these four families were pooled and resulted in a good fit to a 4:48:3:9 trigenic ratio (P between 0.50 and 0.70) (Table VII). These data indicated the presence of three independent genes for resistance to culture TLM in this cross. Since Reichenbachii was shown to have two recessive genes (Tables V and VI), it follows that the third gene came from Marou. The preponderance of Marou infection types (; to 1^+) in the F_2 and backcross F_1 indicate that this resistance gene from Marou is dominant and conditions 0;1 infection types. In the backcross F_1, both recessive genes from Reichenbachii are ineffective as heterozygotes and only the Marou type reactions are expressed. There appeared to be some background effect on the bb allele in Reichenbachii. In DZ04-118 and Marrocos 9623 background this gene pair conditioned a 2 to 3^+ infection types, whereas in Marou the same allele conditioned slightly lower infection types (2 to 2^+). Dyck and Kerber (12) and Knott and Anderson (42) stated

that the genetic background can affect the expression of specific genes and they gave several examples of such genes.

Further evidence that Marou and Reichenbachii have different genes for resistance to culture TLM (race 15) was indicated in the F_2 of Marou/Reichenbachii where non-parental infection types (2 to 2^+ and 4) occurred.

Proposed F_2 genotypes for Marou/Reichenbachii and the backcross F_1, Marou/Reichenbachii//Marou, are given in the Appendix (Tables XVIII and XIX respectively). In all cases encountered, genes governing higher types of resistance appeared epistatic to those controlling a less resistant reaction. The genes from Marou alone gave a 1 type infection. The bb gene pair from Reichenbachii conditioned 2 to 2^+ infection types whereas the aa gene pair conditioned ; to 1^+ infection types. The gene from Marou in combination with the aa gene pair from Reichenbachii conditioned a ; type infection. When the gene from Marou interacted with the bb gene pair from Reichenbachii, infection type 1 developed. Gough and Williams (20), Sunderman and Ausemus (70) and Riede et al. (58) also reported cases where genes governing the higher infection types of resistance were epistatic to those controlling a less resistant reaction.

TABLE VII

SEEDLING REACTIONS OF PARENTS, F_1, F_2 AND BACKCROSS F_1 PLANTS FROM MAROU/REICHENBACHII TO CULTURE TLM OF PUCCINIA GRAMINIS F. SP. TRITICI

Parents or hybrids	Infection types				Total plants
	0	;to1+	2to2+	4	
Marou		10			10
Reichenbachii	10				10
F_1		4			4
F_1 (reciprocal)		4			4
F_2 (observed)	22	299	23	63	407
Ratio (expected)	4	48	3	9	
Expectation	25.4	305.2	19.1	57.2	407
Backcross F_1		97			97

$\chi^2 = 1.9675$
$0.50 < P < 0.70$

Boohai/Reichenbachii

Boohai developed a mesothetic reaction (x=;,1,2,3=) to culture TLM (race 15B) whereas Reichenbachii was completely immune to this culture. The F_1 developed infection types ; and 1. The F_2 population segregated into individual plant reactions varying from complete immunity to susceptibility. A total of 398 F_2 plants derived from four F_1 plants were tested. A chi-square test indicated that the combined data from the four F_1 families fit a 190:57:9 ratio (P value > 0.99) and that data from the different families were homogeneous (P value between 0.95 and 0.99) (Table VIII). This F_2 segregation pattern suggested the presence of four genes for resistance in this cross. As previously noted, Reichenbachii possesses two recessive resistant genes (Tables V and VI). Thus, the other two genes would logically come from Boohai. Since the F_1 infection types resembled those in Boohai rather than those in Reichenbachii, and the F_2 had a preponderance of Boohai infection types, the two genes from Boohai should be dominant. The appearance of infection types 3 and 4 (not present in either parents) in the segregating material indicated that the genes from Boohai and Reichenbachii are not similar.

Under the hypothesis that two recessive genes condition resistance of Reichenbachii those in the heterozygote would be ineffective. So, in the backcross F_1, it was not possible to recover Reichenbachii types and all segregants resembled Boohai (Table VIII). When both recessive resistant genes from Reichenbachii are homozygous they mask the effects of the Boohai genes and the high resistance of Reichenbachii is expressed. In all cases, lower infection types masked higher infection

types (i.e. resistance masked susceptible reaction types). Berg et al. (5) also reported in their studies that higher level of resistance masked genes conditioning lower levels of resistance.

Proposed genotypes for the F_2 and backcross F_1 are given in the Appendix (Tables XX and XXI, respectively). Dominance appeared complete in Boohai and it also appeared that the C- and D- loci gave the same types of infections. Resistance expressed by the two genes from Reichenbachii was very strong and if the two genes from Reichenbachii were homozygous recessive , infection type 0 developed regardless of the genes in Boohai.

TABLE VIII

SEEDLING REACTIONS OF PARENTS, F_1, F_2 AND BACKCROSS F_1 PLANTS FROM BOOHAI/REICHENBACHII TO CULTURE TLM OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

Parents or hybrids	Infection types			Total plants
	0;1⁻to1⁺	2to3⁺	4	
Boohai	10(X⁼;,1,2,3⁼)			10
Reichenbachii	10			10
F_1	4(;,1)			4
F_1 (reciprocal)	4(;,1)			4
F_2 (observed)	295	89	14	398
Ratio (expected)	190	57	9	256
Expectation	295.4	88.6	13.9	398
Backcross F_1	81(1⁻to1⁺)			81

$X^2 = 0.0021$
$P > 0.99$

Cocorit 71/Reichenbachii

Four hundred and two F_2 plants from four F_1 families were tested with culture TLM (race 15B) of Puccinia graminis f.sp. tritici. The seedlings were classified into four groups having infection types 0, ; to 1^+, 2 to 3^+, and 4. The susceptible reaction was represented by infection type 4 and all other infection types represented different levels of resistance. A chi-square test indicated that the combined F_2 data from the F_1 families fit a 16:144:87:9 ratio (P between .70 and 0.90) (Table IX). Data from the different families were also found to be homogeneous (P between 0.95 and 0.99). So, based on the data, the F_2 segregation was indicative of four genes for resistance to culture TLM. Since two resistant genes came from Reichenbachii (Tables V and VI), Cocorit 71 should have contributed the other two genes.

Since all four F_1 plants and 87 backcross F_1s tested (Table IX) developed the same infection type as Cocorit 71 (;), it was assumed that the two genes from Cocorit 71 were dominant. The cross Cocorit 71/Reichenbachii segregated for resistance indicating that the two parents do not have genes for resistance in common. Like the Boohai/Reichenbachii cross, the two recessive genes from Reichenbachii would be ineffective in the heterozygous condition and only the two dominant genes from Cocorit 71 would be expressed in the backcross F_1. As observed in the genotype assignments in the Appendix (Tables XXII and XXIII), the C- and D- loci cause the same type of reaction and dominance appears to be complete in Cocorit 71. Lower infection types again masked higher infection types. The aa and bb loci conditioned infection types ; to 1^+ and 2 to 3^+, respectively. Whenever these two

genes occur together in a homozygous condition immunity is expressed. The C-D- loci appeared to be responsible for infection types 1 to 1^{+}.

TABLE IX

SEEDLING REACTIONS OF PARENTS, F_1, F_2 AND BACKCROSS F_1 PLANTS FROM COCORIT 71/REICHENBACHII TO CULTURE TLM OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

Parents or hybrids	Infection types				Total plants
	0	;to1+	2to3+	4	
Reichenbachii	10				10
Cocorit 71		10(;)			10
F_1		4(;)			4
F_1(reciprocal)		4(;)			4
F_2 (observed)	29	234	126	13	402
Ratio (expected)	16	144	87	9	256
Expectation	25.2	226.1	136.6	14.1	402
Backcross F_1		87			87

$X^2 = 1.7878$
$0.70 < P < 0.90$

Culture MBCT (race 56)

Marrocos 9623/Reichenbachii

Marrocos 9623 was completely susceptible to culture MBCT (infection type 4) while Reichenbachii was highly resistant (infection type 0).The F_1's and reciprocal F_1's had mesothetic types of reactions ($0;13^{=}3^{-}$ and $0;13^{-}4$ respectively). The F_2 segregation pattern of this cross conformed to a 4 resistant : 3 intermediate : 9 susceptible ratio indicative of digenic control (Table X). It was postulated that the aa gene pair suppresses the B locus and the bb gene pair suppresses the A locus, i.e., recessive epistasis. Thus, resistance segregating in the F_2 was attributed to two recessive genes from Reichenbachii. One of the genes (aa) conditioned a ; infection type and the other gene, (bb), $1\text{-}3^{=}$ infection types. Since neither aa or bb singly conditioned an infection type as low as that which developed in Reichenbachii, it is assumed that a slight cumulative effect was obtained when the two gene pairs occurred together. This hypothesis of cumulative interaction between the a and b alleles was further supported in this test by the mesothetic reaction (infection types) of the F_1 plants. However, in the F_2 analysis the mesothetic reactions could not be confidently separated from susceptible ones, whereas the low intermediate reactions ($1 - 3^{=}$) were distinct, they were combined when the data were analyzed. The P value calculated for goodness of fit to the hypothetical ratio of 4:3:9 for seedling reaction of plants in the F_2 were between .50 and .70, supporting the hypothesis that seedling reactions were governed by a two factor pair with susceptibility being dominant.

The F_2 segregation pattern of the reciprocal cross also conformed to a 4 resistant : 3 intermediate : 9 susceptible ratio (Table X), which again indicated digenic control and possible epistasis. This similarity in results between the cross and its reciprocal also indicated that there was no maternal influence on the inheritance of resistance.

The above hypothesis for Marrocos 9623/Reichenbachii and its reciprocal was confirmed by the backcross F_1 data (Marrocos 9623/Reichenbachii//Marrocos 9623). One - fourth of the backcross F_1 plants had mesothetic infection types like the F_1, while the remaining plants were all susceptible.

Since no difference was observed between the F_2 and its reciprocal cross, the data from the two were combined to test the fit to a 4:3:9 ratio. The chi-square tests indicated that the combined data from the eight F_1 families were homogeneous and fit a 4:3:9 ratio (P between .70 and .90) (Table X). The proposed genotypes for the F_2 and reciprocals are given in the Appendix (Table XXIV).

Knott (36,40,41) and Sunderman and Ausemus (70) also have reported cases where resistance to stem rust was controlled by recessive genes.

TABLE X

SEEDLING REACTIONS OF PARENTS, F_1, F_2, RECIPROCALS AND BACKCROSS F_1 PLANTS FROM MARROCOS 9623/REICHENBACHII TO CULTURE MBCT OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

Parents or hybrids	Infection types 0 ;	1-3=	4	Total plants	X^2	P value
Reichenbachii	10			10		
Marrocos 9623			10	10		
F_1	4(X⁻0;13=3⁻)			4		
F_1(recip.)	4(X(0;13⁻4))			4		
F_2	98(0;)	61	210(4+X)	369	1.355	.50-.70
Ratio	4	3	9			
Expectation	92.3	69.2	207.6	369		
F_2(recip.)	91(0;)	73	209(4+X)	373	0.1913	.90-.95
Ratio	4	3	9			
Expectation	93.3	69.9	209.8	373		
F_2 and recip. (pooled)	189(0;)	134	419(4+X)	742	0.2615	.70-.90
Ratio	4	3	9			
Expectation	185.5	139.1	417.4	742		
Backcross F_1	19(X(0;13⁻4))		61	80		

Boohai/Reichenbachii

Boohai developed variable 0;1 infection type with culture MBCT while Reichenbachii was immune (0 infection type). The reaction of F_1 plants (0;) closely resembled that of Boohai. The four F_1 families were analyzed individually in the F_2 and the chi-square for heterogeneity ($P > 0.95$) indicated that the families were homogeneous. Hence, the data from the four families were combined. The F_2 of the four F_1 families was composed of 408 plants which segregated into 309 resistant (0,;,1-3$^=$), 86 moderately resistant (2$^-$ to 2) and 13 susceptible plants (4) (Table XI). The number of plants in the three classes were a satisfactory fit to a 193:54:9 ratio (P between 0.90 and 0.95). These numbers of F_2 plants in the different classes were explained on the basis of four genes. The fact that some plants in the F_2 were more susceptible than the parents, i.e., had higher infection types, indicated that the cultivars possessed different genes for resistance. It was postulated that two recessive genes were contributed by Reichenbachii (Table X), and two dominant ones were contributed by Boohai.

Eighty-eight backcross F_1 progenies derived from four different F_1 families of Boohai/Reichenbachii were tested and classified into only one category (0;1) (Table XI). This would be expected in the backcross-F_1 since both recessive genes from Reichenbachii would be at heterozygous loci and only the dominant resistant genes from Boohai would be effective (Table XXVI)

The F_2 and backcross F_1 data indicate that the expression of aa and bb genes from Reichenbachii are additive with aa and bb singly conditioning ; and 1-3$^=$ infections, respectively, while collectively

they condition immunity. The two dominant genes from Boohai C-D- conditioned 0;1 infection types but in the presence of one homozygous recessive locus C-dd or ccD- they conditioned 2⁻ to 2 infection types. These gene expressions and interactions are illustrated in the genotype assignments in the Appendix (Table XXV). Overall, the genes which conditioned higher levels of resistance were epistatic to those which conditioned lower levels of resistance.

The reciprocal, Reichenbachii/Boohai also responded in the same manner. The chi-square test for heterogeneity indicated that the five F_1 families were homogeneous (P between 0.90 and 0.95) and hence the data were combined to test the fit to a 193:54:9 ratio (Table XI). The chi-square (0.1547) and the P value (between 0.90 and 0.95) indicated that the data were a good fit to this ratio which is indicative of four resistance genes.

Since no differences were observed between Boohai/Reichenbachii and its reciprocal, data from the two crosses were combined for better precision to test the fit to the proposed ratio (Table XI). The heterogeneity chi-square (P value > 0.99) indicated that the data from the nine combined F_1 families were homogeneous and the data were combined. The chi-square for the pooled data was 0.2199 with a P value between 0.75 and 0.90. Thus, it was again ascertained that the data were a good fit to a 193:54:9 ratio supporting the conclusion that four genes controlled resistance in this cross to culture MBCT. The results also indicated no maternal influence.

TABLE XI

SEEDLING REACTIONS OF PARENTS, F_1, F_2, RECIPROCALS AND BACKCROSS F_1 PLANTS FROM BOOHAI/REICHENBACHII TO CULTURE MBCT OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

Parents or hybrids	Infection types			Total plants	X^2	P Value
	0,;,1-3⁻	2⁻to2	4			
Reichenbachii	10(0)			10		
Boohai	10(0;1)			10		
F_1	4			4		
F_1(recip.)	5			5		
F_2	309	86	13	408	0.1317	.90-.95
Ratio	193	54	9	256		
Expectation	307.6	86.1	14.3	408		
F_2(recip.)	383	103	17	503	0.1547	.90-.95
Ratio	193	54	9	256		
Expectation	379.2	106.1	17.7	503		
F_2 and recip. (pooled)	692	189	30	911	0.2199	.75-.90
Ratio	193	54	9	256		
Expectation	686.8	192.2	32.0	911		
Backcross F_1	88(0;1)			88		

Cocorit 71/Reichenbachii

All of the F_2 plants tested from Cocorit 71/Reichenbachii and from the reciprocal cross (Table XII) were as resistant as the parents to culture MBCT, i.e., they developed only 0 to 1 infection types. More than one hypothesis may be advanced to explain these results. Firstly, since neither of the two cultivars developed more than a 1 type reaction when alone, it is possible that Cocorit 71 and Reichenbachii carry the same two genes for resistance to culture MBCT. If only one gene was common to the two varieties, some F_2 segregants probably would have developed more than a type 1 infection. However, acceptance of this hypothesis necessitates an assumption that expression of the double recessive alleles, aabb, may be modified by unidentified background genes since Cocorit 71 and about 18% of the F_2 plants developed higher infection types (0;1) than Reichenbachii (0).

Secondly, it can be hypothesized that the genes in Cocorit 71 are either allelic or very closely linked with genes in Reichenbachii. Kenaschuk et al. (29) and Knott (31) have also reported that the varieties they studied had similar genes for resistance. Knott (34) also has indicated that in his inheritance studies resistance was controlled by linked genes. Concerning allelism, Knott and Srivastava (44) have reported six alleles for resistance to the Sr9 locus.

The backcross F_1 data (Table XII) confirms the results obtained from the F_2 of Reichenbachii/Cocorit 71 and the reciprocal. Of 80 backcross F_1 plants, 77 developed infection types similar to the parents. Three plants developed 2⁻to2 infection types which can be attributed to environmental effects.

TABLE XII

SEEDLING REACTIONS OF PARENTS, F_1, F_2, RECIPROCALS AND BACKCROSS F_1 PLANTS FROM COCORIT 71/REICHENBACHII TO CULTURE MBCT OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

Parents or hybrids	Infection types				Total plants
	0	;	1⁻to1	2⁻to2	
Cocorit 71		10(0;1⁻)			10
Reichenbachii	10(0)				10
F_1		4(0;)			5
F_1 (reciprocal)		4(0;)			5
F_2 (expected)	307	140	26		503
F_2 (reciprocal)	492	12	10		514
Backcross F_1	30	7	40	3	80

DZ04-118/Reichenbachii

DZ04-118 and Reichenbachii developed infection types 2^- to 2 and 0, respectively, when inoculated with culture MBCT. Four F_1 families of DZ04-118/Reichenbachii were tested with culture MBCT (Table XIII). Each family was derived from a single F_1 plant. The plants in each family segregated into four groups of infection types, 0, ;, 1^+ to 2, and 4. The observed numbers in the different classes of the F_2 and reciprocals did not fit any classical genetic ratio. The results may have been modified by unidentified background genes or some kind of gene interaction. When we consider the reaction of DZ04-118 (2^- to 2) to culture MBCT, it is apparent that this cultivar has at least one gene for resistance to this culture. F_3 data is needed to shed light into what is really going on in this cross.

TABLE XIII

SEEDLING REACTIONS OF PARENTS, F_1, F_2, RECIPROCALS AND BACKCROSS F_1 PLANTS FROM DZ04-118/REICHENBACHII TO CULTURE MBCT OF PUCCINIA GRAMINIS F. SP. TRITICI

Parents or hybrids	Infection types				Total plants
	0	;	1+to2	4	
Reichenbachii	10				10
DZ04-118			10(2-to2)		10
F_1	4				4
F_1 (reciprocal)	5				5
F_2 (observed)	301	80	19	8	408
F_2 (reciprocal)	380	100	28	10	518
Backcross F_1	23	20	46		89

Marou/Reichenbachii

Marou had infection types 0;13$^{=}$ whereas Reichenbachii was immune (0 infection type) to culture MBCT. The F_1s and reciprocal F_1s had similar infection types with Reichenbachii. A total of 509 F_2 and 513 reciprocal plants each derived from five F_1 families were tested. Over 90 percent of both the F_2 and reciprocal plants tested were as resistant as Reichenbachii. The remaining plants had infection types ranging from ; to 2^{-} and 4. All 89 of the backcross F_1 plants tested were also immune (0 infection type). The observed numbers in the different classes of the F_2 and reciprocals did not fit any genetic ratios. One reason for this could be misclassification. Low level of infection caused by lower spore viability or change in one of the environmental factors like humidity, temperature, etc. could have also caused this or, simply, the number of F_2 plants used may not have been large enough to detect the number of genes in Marou.

CHAPTER V

SUMMARY AND CONCLUSION

Breeding rust resistant durum wheats is a continuous task since any resistance bred into a cultivar may be masked by the constant shifts or changes in the virulence of the infective pathogen. The development of multigene cultivars, multilines and selective geographical deployment of genes for resistance have been the major approaches used, or proposed, in resistance breeding to slow the loss of effectiveness of resistance genes. For these approaches to succeed, knowledge of the mode of inheritance of the resistance in many sources is necessary.

The objective of this study was to determine the genetic constitution of the durum wheat cultivars 'DZ04-118', 'Marou', 'Boohai', 'Cocorit 71', 'Marrocos 9623', and 'Reichenbachii' relative to factors conditioning their reactions to cultures TLM (race 15B) and MBCT (race 56) of Puccinia graminis f. sp. tritici. The five cultivars were crossed with the variety 'Reichenbachii'. Artificially induced seedling infections were studied in the F_2 and backcross F_1 generations. Attempts were also made through the use of reciprocal crosses to study maternal effects on inheritance of reaction to infection. The results are summarized below:-

1. Two independent recessive genes appeared to control the resistance of 'Reichenbachii' to both cultures TLM and MBCT. When tested with culture TLM, one gene conditioned ; to 1^+ infection types

and the other gene conditioned 2 to 3^+ infection types. These genes interacted cumulatively to condition apparent immunity. The response to culture MBCT was slightly different. One gene conditioned a ; infection type and the other 1 to $3^=$ infection types. In crosses with susceptible 'Marrocos 9623', no additivity was observed between the two genes, but in crosses with resistant 'Boohai' and 'DZ04-118' the action of the two genes together led to immunity. It was not possible from the available data to tell whether the two genes for resistance to TLM and MBCT in 'Reichenbachii' were the same or different. This could be determined by dividing F_3 families into two lots and testing the lots with the two cultures. If the genes are the same, then homozygous and segregating families should react the same to both cultures.

2. 'Marrocos 9623' (P.I. 192334) was completely susceptible (infection type 4) to both cultures TLM and MBCT.

3. The data from DZ04-118/Reichenbachii did not fit any classical genetic ratios when tested with culture MBCT. The result may have been modified by unidentified background gene(s). 'DZ04-118' has no gene for resistance to culture TLM.

4. 'Marou' had one dominant resistant gene to culture TLM. This gene conditioned 0;1 infection types. An intergradation of phenotypes prevented a precise classification of the cross Marou/Reichenbachii when tested with culture MBCT. Thus it was not possible to determine if 'Marou' possessed any resistant genes to culture MBCT.

5. Seedling resistance to culture TLM was governed by two dominant genes in 'Boohai'. These genes acted cumulatively to give 1^- to 1^+ infection types. Individually, both genes conditioned slightly higher infection types (3^- to 3). 'Boohai' developed variable infection types

(0;1^+) when tested with culture MBCT. The results obtained indicated that 'Boohai' had two dominant genes for resistance to culture MBCT each of which conditioned 2^- to 2 infection types.

6. Two dominant genes which individually conditioned 2 to 3^+ infection types, but appeared to have a cumulative effect (1^- to 1^+ infection types), controlled resistance of 'Cocorit 71' to culture TLM. 'Cocorit 71' and 'Reichenbachii' appeared to have either the same two genes for resistance to culture MBCT or genes that were either allelic or closely linked. However, there was some evidence to indicate that there was some background effect, i.e, these genes conditioned complete immunity in 'Reichenbachii' but expressed 0;1^- infection types in 'Cocorit 71'.

7. Throughout seedling trials, genes governing high levels of resistance appeared to be epistatic to those controlling low levels of resistance.

8. In all cases studied, the maternal parent appeared to have no influence on the inheritance studies.

Unfortunately, 'Cocorit 71', 'Boohai' and 'Marou' were not crossed with a susceptible variety. Consequently, the number of genes they carry were deduced only from segregations in crosses with resistant 'Reichenbachii'. Moreover, in segregating generations, variability of infection types on the same leaf and gradations of reactions among seedlings in the same lines made classification difficult in certain crosses, specifically those involving 'Marou'.

These analyses indicated the probable number of genes for resistance in each cultivar to cultures TLM and MBCT of *P. graminis* f. sp. *tritici*, but information regarding the relationships of these genes

to each other and to genes for resistance described previously was incomplete. Diallel crosses between groups of varieties should be used to determine which varieties have genes in common.

Generally, the results reported in this paper show that a number of genes providing satisfactory resistance to cultures TLM (race 15B) and MBCT (race 56) are readily available.

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APPENDIXES

TABLE XIV

PROPOSED F_2 GENOTYPES FOR DZ04-118/REICHENBACHII TESTED WITH CULTURE TLM OF PUCCINIA GRAMINIS F. SP. TRITICI

Phenotypic class	Proposed F_2 genotypes	Ratio
0	1 aabb	1/16
; to 1^+	1 aaBB, 2 aaBb	3/16
2 to 3^+	1 AAbb, 2 Aabb	3/16
4	1 AABB, 2 AABb, 2 AaBB, 4 AaBb	9/16

TABLE XV

PROPOSED GENOTYPES FOR THE BACKCROSS F_1 OF DZ04-118/REICHENBACHII//DZ04-118 TESTED WITH CULTURE TLM OF PUCCINIA GRAMINIS F. SP. TRITICI

AABB (DZ04-118) x aabb (Reichenbachii)

AaBb x AABB (DZ04-118)

Genotype	Infection type
AABB	4
AABb	4
AaBB	4
AaBb	4

* Gene symbols used in each APPENDIX were chosen arbitrarily for illustrative purposes and do not imply allelic relationships with those in other appendixes

TABLE XVI

PROPOSED F_2 GENOTYPES FOR MARROCOS 9623/REICHENBACHII AND ITS RECIPROCAL TESTED WITH CULTURE TLM OF PUCCINIA GRAMINIS F.SP. TRITICI

Phenotypic class	Proposed genotypes of F_2 and reciprocals	Ratio
0	1 aabb	1/16
; to 1^+	1 aaBB, 2 aaBb	3/16
2 to 3^+	1 AAbb, 2 Aabb	3/16
4 to 4^+	1 AABB, 2 AABb, 2 AaBB, 4 AaBb	9/16

TABLE XVII

PROPOSED GENOTYPES FOR THE BACKCROSS F_1 OF MARROCOS 9623/REICHENBACHII//MARROCOS 9623 TESTED WITH CULTURE TLM OF PUCCINIA GRAMINIS F. SP. TRITICI

AABB (Marrocos 9623) X aabb (Reichenbachii)

AaBb x AABB (Marrocos 9623)

Genotype	Infection type
AABB	4
AABb	4
AaBB	4
AaBb	4

TABLE XVIII

PROPOSED F_2 GENOTYPES FOR MAROU/REICHENBACHII TESTED WITH CULTURE TLM OF PUCCINIA GRAMINIS F. SP. TRITICI

; to 1^+ types

1	AABBCC	1	8	AaBbCc	1
2	AABBCc	1	2	AabbCC	1
2	AABbCC	1	4	AabbCc	1
4	AABbCc	1	1	aaBBCC	;
1	AAbbCC	1	2	aaBBCc	;
2	AAbbCc	1	2	aaBbCC	;
2	AaBBCC	1	4	aaBbCc	;
4	AaBBCc	1	1	aaBBcc	;to1^+
4	AaBbCC	1	2	aaBbcc	;to1^+

Total = 48

2 to 2^+ types

1	AAbbcc
2	Aabbcc

Total = 3

0 types

1	aabbCC
2	aabbCc
1	aabbcc

Total = 4

4 types

1	AABBcc
2	AABbcc
2	AaBbcc
4	AaBbcc

Total = 9

TABLE XIX

PROPOSED GENOTYPES FOR THE BACKCROSS F_1 OF MAROU/REICHENBACHII//MAROU TESTED WITH CULTURE TLM OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

AABBCC (Marou) x aabbcc (Reichenbachii)

AaBbCc (F_1) x AABBCC (Marou)

Genotype	Infection type
AABBCC	;,1⁻
AABBCc	;,1⁻
AABbCC	;,1⁻
AABbCc	;,1⁻
AaBBCC	;,1⁻
AABBCc	;,1⁻
AaBbCC	;,1⁻
AaBbCc	;,1⁻

TABLE XX

PROPOSED F_2 GENOTYPES FOR BOOHAI/REICHENBACHII TESTED WITH CULTURE TLM OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

	Genotype	Infection type		Genotype	Infection type
1	AABBCCDD	1^-to1^+	1	aaBBCCDD	;
2	AABBCCDd	1^-to1^+	2	aaBBCCDd	;
2	AABBCcDD	1^-to1^+	1	aaBBCCdd	1^-to1^+
4	AABBCcDd	1^-to1^+	2	aaBBCcDD	;
2	AABbCCDD	1^-to1^+	4	aaBBCcDd	;
4	AABbCCDd	1^-to1^+	2	aaBBCcdd	1^-to1^+
4	AABbCcDD	1^-to1^+	1	aaBBccDD	1^-to1^+
8	AABbCcDd	1^-to1^+	2	aaBBccDd	1^-to1^+
1	AAbbCCDD	;	2	aaBbCCDD	;
2	AAbbCCDd	;	4	aaBbCCDd	;
1	AAbbCCdd	1^-to1^+	2	aaBbCCdd	1^-to1^+
2	AAbbCcDD	;	4	aaBbCcDD	;
4	AAbbCcDd	;	8	aaBbCcDd	;
2	AAbbCcdd	1^-to1^+	4	aaBbCcdd	1^-to1^+
1	AAbbccDD	1^-to1^+	2	aaBbccDD	1^-to1^+
2	AAbbccDd	1^-to1^+	4	aaBbccDd	1^-to1^+
2	AaBBCCDD	1^-to1^+	1	aabbCCdd	0
4	AaBBCCDd	1^-to1^+	2	aabbCcdd	0
4	AaBBCcDD	1^-to1^+	1	aabbccDD	0
8	AaBBCcDd	1^-to1^+	2	aabbccDd	0
4	AaBbCCDD	1^-to1^+	1	aabbCCDD	0
8	AaBbCCDd	1^-to1^+	2	aabbCCDd	0
8	AaBbCcDD	1^-to1^+	2	aabbCcDD	0
16	AaBbCcDd	1^-to1^+	4	aabbCcDd	0
2	AabbCCDD	;	1	aabbccdd	0
4	AabbCCDd	;	2	aaBbccdd	;$to1^+$
2	AabbCCdd	1^-to1^+	1	aaBBccdd	;$to1^+$
4	AabbCcDd	;	2	AabbccDD	1^-to1^+
8	AabbCcDd	;	4	AabbccDd	1^-to1^+
4	AabbCcdd	1^-to1^+			

Total = 190

TABLE XX (CONTD.)

Genotype	Infection type	Genotype	Infection type
1 AABBCCdd	3^-to3	2 AaBBccDD	3^-to3
2 AABBCcdd	3^-to3	4 AaBBccDd	3^-to3
1 AABBccDD	3^-to3	4 AaBbCCdd	3^-to3
2 AABBccDd	3^-to3	8 AaBbCcdd	3^-to3
2 AABbCCdd	3^-to3	4 AaBbccDD	3^-to3
4 AABbCcdd	3^-to3	8 AaBbccDd	3^-to3
2 AABbccDD	3^-to3	2 Aabbccdd	$2to3^+$
4 AABbccDd	3^-to3	1 AAbbccdd	$2to3^+$
2 AaBBCCdd	3^-to3	4 AaBBCcdd	3^-to3

Total = 57

Genotypes	Infection type
1 AABBccdd	4
2 AABbccdd	4
2 AaBBccdd	4
4 AaBbccdd	4

Total = 9

TABLE XXI

PROPOSED GENOTYPES FOR THE BACKCROSS F_1 OF BOOHAI/ REICHENBACHII//BOOHAI TESTED WITH CULTURE TLM OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

(Boohai) AABBCCDD x (Reichenbachii) aabbccdd

AaBbCcDd x AABBCCDD

Genotype	Infection type	Genotype	Infection type
AABBCCDD	$1^{-}to1^{+}$	AaBBCCDD	$1^{-}to1^{+}$
AABBCCDd	$1^{-}to1^{+}$	AaBBCCDd	$1^{-}to1^{+}$
AABBCcDD	$1^{-}to1^{+}$	AaBBCcDD	$1^{-}to1^{+}$
AABBCcDd	$1^{-}to1^{+}$	AaBBCcDd	$1^{-}to1^{+}$
AABbCCDD	$1^{-}to1^{+}$	AaBbCCDD	$1^{-}to1^{+}$
AABbCCDd	$1^{-}to1^{+}$	AaBbCCDd	$1^{-}to1^{+}$
AABbCcDD	$1^{-}to1^{+}$	AaBbCcDD	$1^{-}to1^{+}$
AABbCcDd	$1^{-}to1^{+}$	AaBbCcDd	$1^{-}to1^{+}$

TABLE XXII

PROPOSED F_2 GENOTYPES FOR COCORIT 71/REICHENBACHII TESTED WITH CULTURE TLM OF PUCCINIA GRAMINIS F. SP. TRITICI

; to 1^+ types				2to3^+ types			
1	AABBCCDD	2	AabbCCDD	1	AABBCCdd	2	AaBBccDD
2	AABBCCDd	4	AabbCCDd	2	AABBCcdd	4	AaBBccDd
2	AABBCcDD	1	aaBBCCDD	1	AABBccDD	4	AaBbCCdd
4	AABBCcDd	2	aaBBCCDd	2	AABBccDd	8	AaBbCcdd
2	AABbCCDD	1	aaBBCCdd	2	AABbCCdd	4	AaBbccDD
4	AABbCCDd	2	aaBBCcDD	4	AABbCcdd	8	AaBbccDd
4	AABbCcDD	4	aaBBCcDd	2	AABbccDD	2	AabbCCdd
8	AABbCcDd	2	aaBBCcdd	4	AABbccDd	4	AabbCcDD
1	AAbbCCDD	1	aaBBccDD	1	AAbbCCdd	8	AabbCcDd
2	AAbbCCDd	2	aaBBccDd	2	AAbbCcdd	4	AabbCcdd
2	AAbbCcDD	1	aaBBccdd	1	AAbbccDD	2	AabbccDD
4	AAbbCcDd	2	aaBbCCDD	2	AAbbccDd	4	AabbccDd
2	AaBBCCDD	4	aaBbCCDd	2	AaBBCCdd	1	AAbbccdd
4	AaBBCCDd	2	aaBbCCdd	4	AaBBCcdd	2	Aabbccdd
4	AaBBCcDD	4	aaBbCcDD				
8	AaBBCcDd	8	aaBbCcDd				
4	AaBbCCDD	4	aaBbCcdd				
8	AaBbCCDd	2	aaBbccDD				
8	AaBbCcDD	4	aaBbccDd				
16	AaBbCcDd	2	aaBbccdd				
Total = 144				Total = 87			

4 types		0 types	
1	AABBccdd	1	aabbCCDD
2	AABbccdd	2	aabbCCDd
2	AaBBccdd	1	aabbCCdd
4	AaBbccdd	2	aabbCcDD
Total = 9		4	aabbCcDd
		2	aabbCcdd
		1	aabbccDD
		2	aabbccDd
		1	aabbccdd
		Total = 16	

TABLE XXIII

PROPOSED GENOTYPES FOR THE BACKCROSS-F_1 OF COCORIT 71/ REICHENBACHII//COCORIT 71 TESTED WITH CULTURE TLM OF PUCCINIA GRAMINIS F. SP. TRITICI

Genotype	Infection type	Genotype	Infection type
AABBCCDD	1^-to1^+	AaBBCCDD	1^-to1^+
AABBCCDd	1^-to1^+	AaBBCCDd	1^-to1^+
AABBCcDD	1^-to1^+	AaBBCcDD	1^-to1^+
AABBCcDd	1^-to1^+	AaBBCcDd	1^-to1^+
AABbCCDD	1^-to1^+	AaBbCCDD	1^-to1^+
AABbCCDd	1^-to1^+	AaBbCCDd	1^-to1^+
AABbCcDD	1^-to1^+	AaBbCcDD	1^-to1^+
AABbCcDd	1^-to1^+	AaBbCcDd	1^-to1^+

TABLE XXIV

PROPOSED F_2 GENOTYPES FOR MARROCOS 9623/REICHENBACHII AND IT'S RECIPROCAL TESTED WITH CULTURE MBCT OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

Phenotypic class	Proposed F_2 genotypes	Ratio
0;	1 aaBB, 2 aaBb, 1 aabb	4/16
Intermediate(1-3=) 4 and X[a]	1 AAbb, 2 Aabb	3/16
	1 AABB, 2 AABb, 2 AaBB, 4 AaBb	9/16

[a]X refers to mesothetic infection types.

TABLE XXV

PROPOSED F_2 GENOTYPES FOR BOOHAI/REICHENBACHII TESTED WITH CULTURE MBCT OF *PUCCINIA GRAMINIS* F. SP. *TRITICI*

Genotype	Infection types	Genotype	Infection types
1 AABBCCDD	0;1	2 AabbccDD	1-3=
2 AABBCCDd	0;1	4 AabbccDd	1-3=
2 AABBCcDD	0;1	1 aaBBCCDD	;
4 AABBCcDd	0;1	2 aaBBCCDd	;
2 AABbCCDD	0;1	1 aaBBCCdd	;
4 AABbCCDd	0;1	2 aaBBCcDD	;
4 AABbCcDD	0;1	4 aaBBCcDd	;
8 AABbCcDd	0;1	2 aaBBCcdd	;
1 AAbbCCDD	0;1	1 aaBBccDD	;
2 AAbbCCDd	0;1	2 aaBBccDd	;
1 AAbbCCdd	1-3=	1 aaBBccdd	;
2 AAbbCcDD	0;1	2 aaBbCCDD	;
4 AAbbCcDd	0;1	4 aaBbCCDd	;
2 AAbbCcdd	1-3=	2 aaBbCCdd	;
1 AAbbccDD	1-3=	4 aaBbCcDD	;
2 AAbbccDd	1-3=	8 aaBbCcDd	;
2 AaBBCCDD	0;1	4 aaBbCcdd	;
4 AaBBCCDd	0;1	2 aaBbccDD	;
4 AaBBCcDD	0;1	4 aaBbccDd	;
8 AaBBCcDd	0;1	2 aaBbccdd	;
4 AaBbCCDD	0;1	1 aabbCCDD	0
8 AaBbCCDd	0;1	2 aabbCCDd	0
8 AaBbCcDD	0;1	1 aabbCCdd	0
16 AaBbCcDd	0;1	2 aabbCcDD	0
2 AabbCCDD	0;1	4 aabbCcDd	0
4 AabbCCDd	0;1	2 aabbCcdd	0
2 AabbCCdd	1-3=	1 aabbccDD	0
4 AabbCcDD	0;1	2 aabbccDd	0
8 AabbCcDd	0;1	1 aabbccdd	0
4 AabbCcdd	1-3=	1 AAbbccdd	1-3=
2 Aabbccdd	1-3=		

Total = 193

TABLE XXV (CONTD.)

Genotype	Infection type	Genotype	Infection type
1 AABBCCdd	2⁻to2	4 AaBBCcdd	2⁻to2
2 AABBCcdd	2⁻to2	2 AaBBccDD	2⁻to2
1 AABBccDD	2⁻to2	4 AaBBccDd	2⁻to2
2 AABBccDd	2⁻to2	4 AaBbCCdd	2⁻to2
2 AABbCCdd	2⁻to2	8 AaBbCcdd	2⁻to2
4 AABbCcdd	2⁻to2	4 AaBbccDD	2⁻to2
2 AABbccDD	2⁻to2	8 AaBbccDd	2⁻to2
4 AABbccDd	2⁻to2		
2 AaBBCCdd	2⁻to2		
Total = 54			

Genotype	Infection type
1 AABBccdd	4
2 AABbccdd	4
2 AaBBccdd	4
4 AaBbccdd	4
Total = 9	

TABLE XXVI

PROPOSED GENOTYPES FOR THE BACKCROSS F_1 OF BOOHAI/ REICHENBACHII//BOOHAI TESTED WITH CULTURE MBCT OF PUCCINIA GRAMINIS F. SP. TRITICI

(Boohai)		(Reichenbachii)
AABBCCDD	x	aabbccdd

AaBbCcDd x AABBCCDD

Genotype	Infection type	Genotype	Infection type
AABBCCDD	0;1	AaBBCCDD	0;1
AABBCCDd	0;1	AaBBCCDd	0;1
AABBCcDD	0;1	AaBBCcDD	0;1
AABBCcDd	0;1	AaBBCcDd	0;1
AABbCCDD	0;1	AaBbCCDD	0;1
AABbCCDd	0;1	AaBbCCDd	0;1
AABbCcDD	0;1	AaBbCcDD	0;1
AABbCcDd	0;1	AaBbCcDd	0;1

VITA

Efrem Bechere

Candidate for the Degree of

Doctor of Philosophy

Thesis: INHERITANCE OF RESISTANCE TO PHYSIOLOGIC RACES 15B (CULTURE TLM) AND 56 (CULTURE MBCT) OF STEM RUST (PUCCINIA GRAMINIS F. SP. TRITICI) IN SIX DURUM WHEAT (TRITICUM DURUM DESF.) CULTIVARS

Major Field: Crop Science

Biographical:

Personal Data: Born in Shoa, Ethiopia, on September 15, 1952, the son of Ato Bechere Abebe and W/o Fetenech Abdi.

Education: Graduated from Teferi Makonnen High School, Addis Ababa, Ethiopia, in May 1969; received the Bachelor of Science Degree in Plant Science from Addis Ababa University, Alemaya, Ethiopia, in September 1977; received the Master of Science degree in Agronomy from Addis Ababa University, Alemaya, Ethiopia, in July 81; and completed the requirements for the Doctor of Philosophy degree in Crop Science at Oklahoma State University in December, 1987.

Professional Experience: Graduate assistant, 1977 - 1979; Assistant lecturer, 1979 - 1980; Lecturer and wheat breeder 1980 - 1983, at Debre Zeit Junior College of Agriculture and Research Center, Debre Zeit, Ethiopia; Head, Department of Crop Science and Coordinator of the National Durum Wheat Program, 1983 - 1984, at Debre Zeit Junior College of Agriculture and Research Center; Fulbright scholar, Oklahoma State University, from August 1984 to December 1987.

Professional Organizations: Graduate Student Member, American Society of Agronomy and Crop Science Society of America, Gamma Sigma Delta - The Honor Society of Agriculture.