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Title: Inheritance of Durable Type Disease Resistance to Leaf Rust in Wheat (Triticum aestivum L.em Thell)

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Wheat cultivars bred with vertical resistance genes to leaf rust (Puccinia recondita f.sp. tritici) are often short-lived due to rapid build up of virulent races of the rust pathogen. Slow rusting resistance has been reported to be a more durable type of resistance. To exploit the advantages of this durability, genetic analysis of slow rusting resistance is essential. Two experiments were conducted to determine the inheritance of slow leaf rusting and three of its components in wheat.

F_6 progenies derived from a diallel cross involving one fast rusting and five slow rusting wheat genotypes were evaluated along with the parents in the field under epidemics initiated by artificial inoculation. The area under leaf rust progress curve (AULRPC) was used to measure the rust severity over time.

Differences in the AULRPC were observed among crosses and among progenies within crosses. Transgressive segregation toward greater susceptibility was observed with the distribution of the progeny being skewed toward resistance. Predominantly additive gene action including additive X additive epistasis for slow rusting reaction was detected. The number of genes

controlling slow rusting resistance varied from two to four, depending on the parents used in the cross. The association between slow rusting and plant maturity was low and negative and no relationship of plant height with slow rusting was observed.

The inheritance and associations of three components of slow rusting viz. latent period, receptivity, and uredium size were studied in one of the crosses involving a fast and a slow rusting parent. Forty F_6 lines, two parents, and a susceptible check cultivar were inoculated with a single leaf rust race and evaluated in the greenhouse. Narrow-sense heritability estimates were moderately high for all the components. Estimates of number of genes were two or three for latent period and three or four for uredium size and receptivity. Genotypic and phenotypic correlations between latent period and uredium size were high and negative. The association of receptivity was intermediate and negative with latent period and low and positive with uredium size. Final rust severity (FRS) and AULRPC obtained from the field study with common entries were associated negatively with latent period and positively with uredium size.

Since slow rusting resistance and its components are controlled by a few genes and have moderately high narrow-sense heritability estimates, early generation selection should be effective for these traits. Slow rusting genotypes can be selected on the basis of resistance components in the greenhouse and low AULRPC or FRS in the field.

INHERITANCE OF DURABLE TYPE DISEASE RESISTANCE TO LEAF RUST IN WHEAT (Triticum aestivum L.em Thell)

by

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Typed by Modan Das

In dedication to:

my parents, Madhab and Susheila Das

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INTRODUCTION

Leaf rust caused by Puccinia recondita f.sp.tritici is one of the most destructive and widely distributed diseases of wheat (Triticum aestivum L.). The most effective and economical method to control leaf rust is through breeding resistant cultivars (Caldwell, 1968). Resistant wheat cultivars bred with race-specific, vertical resistance (Vanderplank, 1963) genes are overcome by rust due to rapid build up of virulent races of the rust pathogen. Therefore, a more durable type of resistance is required to reduce wheat yield losses from leaf rust. Slow rusting resistance of wheat has been reported to be a more durable type of resistance (Caldwell, 1968; Kuhn et al. 1978; Rajaram et al. 1984) and has been identified for leaf rust (Caldwell et al. 1970; Gavinlertvatana and Wilcoxson, 1978; Milus and Line, 1980; Rajaram et al. 1984; Bjarko and Line 1988a, 1988b). Slow rusting is a form of resistance where the host expresses a susceptible disease reaction but disease development is slower when compared to a susceptible genotype (Caldwell, 1968). Such resistance is the product of an interaction of the host and pathogen at different stages of pathogenesis which can be expressed as different components of resistance. The important components of slow rusting resistance are latent period, receptivity (number of uredia per unit area of leaf), uredium size, and spore production (Parlevliet, 1979).

Slow leaf rusting has been reported (Gavinlertvatana and Wilcoxson, 1978) to be polygenic with high narrow-sense heritability. In contrast, Bjarko and Line (1988b) found that the inheritance of slow leaf rusting in wheat was oligogenic with high narrow-sense heritability estimates. Gene action for slow rusting resistance to leaf rust has been reported to be additive without any dominance interaction in one slow rusting wheat cultivar, while in another slow rusting cultivar the gene action was best explained by additive X additive interaction (Bjarko and Line, 1988a). Slow rusting resistance to stem rust was estimated to be controlled by 2 to 12 genes with predominantly additive gene action (Skovmand et al. 1978). Ayers et al. (1981) reported quantitative inheritance of slow rusting resistance to stem rust of wheat.

There are also reports on the inheritance and association of the components of slow rusting to leaf rust in wheat (Kuhn et al. 1980; Lee and Shaner, 1985a; 1985b; Singh et al. 1990). However, these studies focus mainly on the inheritance of latent period and the association of latent period with other components. Latent period has also been reported to be highly correlated with the slow disease development in the field (Shaner and Finney, 1980; Singh et al. 1990).

To exploit the advantages of more durable resistance offered by slow rusting, more information on the nature of inheritance of slow rusting and its components and possible associations among them are necessary. Furthermore, efficient selection for slow rusting genotypes requires development of methods for both greenhouse and field evaluations that are fast and reliable at seedling and mature plant stages in the early generation materials.

International Maize and Wheat Improvement Center (CIMMYT) derived wheat cultivars are grown on more than 50.7 million hectares worldwide (Dalrymple, 1986). In a global context, durable disease resistance and genetic diversity are of paramount importance in the CIMMYT breeding program (Rajaram et al. 1988). CIMMYT routinely identifies slow rusting lines in the field and greenhouse (Rajaram et al. 1988; Singh et al. 1990). Genetic analysis of slow rusting and its components would strengthen the concept that CIMMYT wheats can avoid epidemics and would help in designing suitable methods for incorporation of slow rusting resistance genes in future cultivars.

The objectives of this study were to determine: 1) the nature of inheritance of slow rusting resistance to leaf rust and its components, 2) associations among components of slow rusting and correlation of the components with slow disease development in the field, and 3) the relationships of slow rusting with cultivar maturity and plant height in CIMMYT spring wheats.

The study is presented in the form of two manuscripts in two chapters each consisting of a separate abstract, introduction, materials and methods, results and discussion, and references followed by a common conclusion and a bibliography.

REVIEW OF LITERATURE

Nature of Slow Rusting Resistance

Disease resistance in plants is often divided into two types. One type is associated with a host cell hypersensitivity reaction. This results in the death of the cells or chlorosis and impaired plant development. This has been designated by an array of names including major-gene, monogenic, race-specific, hypersensitive, and vertical resistance. The second type of resistance is characterized by a reduced rate of epidemic development despite the expression of a susceptible host reaction. This has been designated as general, partial, minor gene, non-race-specific, and horizontal resistance. True slow rusting resistance falls under the latter category of disease resistance (Caldwell, 1968; Rajaram et al., 1984; Parlevliet, 1988).

Non-Race-Specificity

Contradictory results have been obtained from the studies regarding the non-race-specificity of slow rusting resistance. Kuhn et al. (1978) studied the response of two slow rusting ('P6028' and 'Suwon 85') and two fast rusting ('Suwon 92'and 'Monon') winter wheat cultivars to 22 isolates of leaf rust Puccinia recondita f. sp. tritici. They measured the development of the isolates on these four wheat cultivars in growth chambers. For a given isolate of the pathogen, only cultivars that developed a susceptible reaction type were compared. Thus, the development of five isolates on 'P6028'and 21 isolates on 'Suwon 85', were compared as to their development on Monon and Suwon 92.

For all five isolates on P6028, and for 17 isolates on Suwon 85, the latent periods were longer, a lower percentage of infection sites developed into pustules, and there were fewer pustules per unit area of leaf than on Suwon 92 and Monon. The other four isolates were exceptions to these trends because of greater level of resistance by Monon and Suwon 92. The development of these four isolates on Suwon 85 was similar to the expression of the other 17 isolates on this cultivar. This showed that slow leaf rusting resistance was race-non-specific.

Milus and Line (1980) reported that components of slow leaf rusting resistance for wheat cultivars 'Borah', 'Wampum', and 'Wandell' were consistently culture specific. On Borah and Wampum, Culture 2 had a shorter latent period, more infections with sporulations, more spores per uredium, and higher infection types than did Culture 1. The opposite response was observed with the cultivar Wandell. Specificity to cultures of wheat leaf rust has also been reported by Browder and Eversmeyer (1987) in the slow rusting cultivar Suwon 85, especially at low temperatures (5°C to 12°C).

In a glasshouse experiment, Parlevliet (1975) investigated the latent periods in six barley cultivars which were inoculated with five isolates of the barley leaf rust (Puccinia hordei) pathogen. The latent period with one of the isolates was about a half day shorter than for the other four. Difference in the duration of the latent period was more pronounced in cultivars thought to represent slow rusting types.

Durability

Durable disease resistance in plants has been defined as resistance that remains effective in widely cultivated genotypes (Johnson 1981). Durability of resistance is thought to be best judged over time. Caldwell (1968) drew attention of wheat scientists to general resistance to rusts, emphasizing its durability. Slow rusting resistance is considered to be durable, but pertinent information is scant. The slow rusting reaction in the wheat cultivar 'Knox' to leaf rust has been effective for some 20 years (Ohm and Shaner, 1976). Similarly, Mexican cultivars 'Torim 73' and 'Pavon 76' have maintained their slow rusting reaction for the last 15 and 12 years, respectively (Rajaram et al.1988).

Many West European barley cultivars have good levels of partial resistance to barley leaf rust (Parlevliet et al.1980). Habgood and Clifford (1981), when considering the English experience, concluded that partial resistance of barley to leaf rust is durable enough to be useful. Other indications that partial resistance can be considered durable came from studies where old and new cultivars were compared. In areas of the United States where breeders did not exploit specific resistance in wheat to leaf rust, modern cultivars have less rust than the older cultivars indicating that an accumulation of partial resistance has occurred (Young 1970).

Rajaram et al. (1988) mentioned that the widespread adoption of CIMMYT-derived semidwarf wheat cultivars on more than 50 million ha worldwide is due, in part, to durable resistance against rust diseases. They suggested that these wheat genotypes contain genes for partial resistance in conjunction with major genes. They have also noted that the high yield potential

of semidwarf wheats would have been short-lived if stable resistance to the rust diseases had not been simultaneously bred in.

Measuring Slow Rusting Resistance

The slow rusting type of resistance was noted in wheat even before the demonstration by Biffen (1905) that disease resistance in plants, like other traits, is heritable. Farrer (1898) observed that rust increase proceeds more slowly during the growing season in some cultivars than in others although at maturity the cultivars may show equal amount of infection.

In the epidemics of race 15B of Puccinia graminis f.sp. tritici, produced by artificially applying spore showers on wheat cultivars, Hayden (1956) observed that the cultivars 'Lee' and 'Sentry' were less damaged than the cultivars 'Marquis', 'Mida', 'Carleton', and 'Nugget'. But on the basis of infection type all the cultivars were susceptible. However, without the knowledge of infection rate (r) and other methods of identification, he was not in a position to appreciate its significance (Vanderplank, 1960). Vanderplank's (1960, 1963) mathematical approach to analysis of epidemics suggested the requirement of slower infection rate, i.e., lower 'r' value for the characterization of slow rusting, and subsequently this criterion has been used for identifying slow rusting in cultivars.

Wilcoxson et al. (1975) used two parameters: area under the disease progress curve (AUDPC) and Vanderplank's (1963) 'r' value for evaluating slow rusting resistance of wheat cultivars to stem rust. Area under the disease progress curve reflects both severity and rate of disease development. They found AUDPC values reliable and convenient for computation. By this method,

differences among the cultivars were distinct and consistent from trial to trial. Vanderplank (1963) suggested that r-values were most accurately estimated during the early phases of disease development.

In the measurement of slow rusting, the proportion of host tissue affected by the disease is measured. This is called a disease severity (DS) measurement. This can be done either once near the end or several times during the development of the epidemic. The former is assumed to represent the cumulative result of the components of slow rusting over time (Parlevliet and Van Ommeren, 1975). The latter makes it possible to calculate the AUDPC or the infection rate, r.

Rees et al. (1979) compared various methods and concluded that r value was the least suitable parameter to describe slow rusting of the cultivars. Shaner and Finney (1980) also found that the AUDPC was a better criterion to measure partial resistance than the infection rate, r.

Parlevliet (1987) reported a comparison of infection rate (r), disease severity (DS), and AUDPC in the assesment of partial resistance of wheat to leaf rust. He suggested that the r value not only requires more computation, but it is apparently also a poor estimator of partial resistance and only poorly correlated with the components of partial resistance. Disease severity and AUDPC appeared to be much better parameters to measure partial resistance. Both methods were highly correlated with one another and with components of partial resistance. One assesment is needed for DS while several are required for AUDPC.

Components of Slow Rusting

Slow rusting resistance as measured by 'r' or AUDPC values is the end product of an interaction of the host and pathogen at different stages of pathogenesis. Cultivars may differ in their ability to retard development of disease because they may possess different combinations of the component factors that ultimately lead to the expression of slow rusting. The important components of slow rusting are: receptivity (number of pustules per unit area of host surface), latent period, uredium size, and spore production (Ohm and Shaner, 1976; Parlevliet, 1979).

Receptivity

Receptivity was one of the earliest recognized components of slow rusting. Hayden (1956) suggested that wide differences among cultivars early in the growing season for initial infectibility can be potentially important in determining subsequent rust damage. Caldwell (1970) used uredium number on the flag leaves as the criterion for evaluating slow leaf rusting in wheat.

Ohm and Shaner (1976) found that the slow rusting cultivar Suwon 85 had significantly fewer uredia per square centimeter of leaf area after uniform inoculation with leaf rust than the two fast rusting cultivars Suwon 92 and Monon. Kuhn et al. (1978) also reported production of fewer uredia per unit area of leaf on slow rusting in comparison to fast rusting cultivars. A similar result has also been reported by Milus and Line (1980) with leaf rust in the wheat cultivars Borah and Wampum. Rajaram et al. (1988) have reported a significantly decreased number of uredia per unit area of leaf surface in a

number of CIMMYT-derived wheat cultivars/lines as compared to the fast rusting cultivars like 'Inia 66', 'Siete Cerros', and 'Morocco'. Singh et al. (1990) reported a 98% reduced receptivity in a slow rusting spring wheat selection CM84833-3M-0Y-0M-9Y-0M as compared to the fast rusting wheat cultivar Morocco.

Latent Period

Latent period is the time between inoculation and uredial spore production. Latent period is the most important component of partial resistance in wheat and barley leaf rust (Parlevliet, 1988). Lee and Shaner (1984) have suggested that latent period can be used as a good criterion for selecting wheat cultivars for slow rusting. When compared to the other components of slow rusting, latent period can be measured with the smallest error (Parlevliet, 1987). Rajaram et al. (1988) have reported a significantly longer latent period in the slow rusting cultivars 'Seri 82' and 'Genero 81' in comparison to the fast rusting cultivars Morocco and Siete Cerros when inoculated with same isolate of leaf rust. Singh et al. (1990) have observed a 79% increased latent period in the CIMMYT spring bread wheat selection CM84833-3M-0Y-0M-9Y-0M in comparison to the fast rusting cultivar Morocco.

Parlevliet (1975) observed that plant growth stage and the age of the leaves can play an important role in influencing latent period. The relative latent period measured on seedlings did not adequately predict the latent period measured on adult plants. This indicates that results from seedling tests for latent period must be interpreted with caution.

Uredium size

Generally, small uredia means less spores per uredium. The smaller uredium size of slow rusting cultivars in comparison to fast rusting cultivars has been observed in a number of studies with wheat leaf rust (Singh et al. 1990, Rajaram et al. 1988; Shaner et al. 1978; Ohm and Shaner, 1976). Ohm and Shaner (1976) found that uredia on slow rusting cultivars were four- to six-tenths the size of those on fast rusting cultivars. Singh et al. (1990) reported a 78% reduction in uredium size in a slow leaf rusting wheat selection CM84833- 3M-0Y-0M-9Y-0M as compared to the fast rusting cultivar Morocco.

Spore production

Spore production (SP) can be expressed in various ways, i.e., SP per unit leaf area, SP per uredium, SP per unit area of lesion, or SP per unit area of sporulating host surface (Parlevliet, 1985). The SP per unit area can be measured in units of time or over the entire infectious period. Spore production, expressed as number of spores per square centimeter of leaf per day is the combined effect of uredium size, spores produced per unit area of uredium, and number of uredia per square centimeter of leaf (Shaner et al. 1978). Shaner et al. (1978) observed that the slow leaf rusting wheat cultivar Suwon 85 produced fewer numbers of spores, mainly because of smaller uredia. When sporulation was expressed as the number of spores per unit area of uredium, it was similar with the fast rusting cultivars Monon and Suwon 92. However, the other slow rusting cultivar P6028 produced fewer number of urediospores both due to lower spore production per unit area of uredium and a smaller uredium. They

also found that fast rusters produced two to three times more inoculum than slow rusters.

Effect of Temperature on Slow Rusting

The influence of temperature on the development of leaf rust on the slow rusting cultivar Suwon 85 was studied by Browder and Eversmeyer (1987). They inoculated seedlings of Suwon 85 and the fast rusting cultivar 'Thatcher' with four uredial cultures of leaf rust; the experimental material was then grown at 5, 12, 19, and 26°C in a growth chamber. They could not find a classifiable difference in the infection type (IT) between the two cultivars with any of the four cultures at 19 or 26°C. However, a consistent difference in the infection type between Suwon 85 and Thatcher with the same culture was observed at 5 and 12°C.

Kaul and Shaner (1989) studied the effect of temperature on adult-plant resistance to leaf rust in wheat. They evaluated several wheat breeding lines and three cultivars grown in the greenhouse/growth chamber under various diurnal temperatures, ranging from 15/12 to 30/21°C (day/night). Plants were inoculated with a pure culture of leaf rust after flag leaves had emerged. The susceptible control, Morocco, was consistently susceptible, with an IT of 3+. Temperature induced major differences in ITs in all but three lines with adult-plant resistance, which were of IT 0 or IT 0c at all temperatures. None of the lines developed a susceptible reaction (IT 3+) at the lowest temperature regime, whereas all temperature-sensitive lines developed at least a few IT of 3+ uredia at the highest temperature regime.

The effect of temperature on latent period of slow rusting (Texas lines '78V2950', '78V2905', and 71A894-2') and fast rusting (cultivars 'Palo Duro', 'Danne', 'TAM W-103', and 'TAM W-101') winter wheat genotypes infected with leaf rust was studied at temperatures 4, 10, 16, 21, and 27°C by Johnson (1980) in growth chamber experiments. The latent period increased as the temperature decreased, but the latent period of the slow rusting lines increased more than that of the faster rusting lines. Pretorius et al. (1988) also observed a longer latent period at 15°C than at 21°C in wheat leaf rust system.

Relationship Between Slow Rusting and Adult Plant Resistance

Adult plant resistance can be defined as resistance absent in seedlings but is expressed in adult stage of the plant (Rajaram, 1972; Vanderplank, 1982). Thus genes for adult plant resistance are expressed only in adult plants. Rajaram (1972) developed a method for detection and evaluation of adult plant resistance to stem rust in wheat. This method consists of testing wheat genotypes both in the greenhouse (seedling stage) and field (adult stage) with a large number of isolates of the pathogen. He inoculated 16 varieties of wheat with 200 isolates from the Yaqui valley of Mexico and 148 isolates from Toluca of Mexico. The Yaqui valley and Toluca are separated by 1800 kilometers with quite different climatic conditions. The varieties 'Pitic 62' and 'Penjamo 62' were highly susceptible in both seedling and adult stages. However, the varieties 'Ciano 67', 'Lerma Rojo', and 'Hopps' were susceptible as seedling to a large number of isolates but were highly resistant in adult stage in both Yaqui valley and Toluca. This resistance was due to genes for adult plant resistance. Some

adult plant resistance also has the slow rusting characteristics. Woodend (1977) (cited in Knott, 1988) tested five wheat lines with adult plant resistance to stem rust. Compared to the susceptible check, they generally showed reduced rust severity, uredium size, and area under the disease progress curve.

Slow rusting resistance can also be expressed in the seedlings. Data presented by Rajaram et al. (1988) showed that slow leaf rusting cultivars 'Juzco', 'Kathadin', and 'Pavon 76', had significantly reduced uredium size and receptivity as compared to the susceptible check Inia 66 in both seedling and adult plant stages of growth.

Inheritance of Slow Rusting

Gavinlertvatana and Wilcoxson (1978) studied the inheritance of slow rusting of spring wheat to leaf rust using F5 progenies derived from a diallel cross of the cultivars 'Thatcher', 'Marquis', and 'Lee'. Reciprocal crosses were not included. They evaluated slow rusting in a natural epidemic of leaf rust races UN2 and UN17. Narrow-sense heritability estimates ranged from 55 to 87% with between 3 and 21 genes affecting slow rusting resistance.

The nature of gene action for resistance to leaf rust was studied by Bjarko and Line (1988a). They used parents, F1, F2, and backcross populations from crosses of two slow leaf rusting cultivars Borah and Wampum, a highly resistant cultivar Wared, and a susceptible cultivar Twin. Resistance in Wared was expressed by a low infection type usually accompanied by necrosis. Inheritance of resistance as measured by AUDPC was recessive in Borah and partially recessive in Wampum and Wared. They used the joint scaling test

described by Mather and Jinks (1982) to determine the gene action of leaf rust resistance in each resistant parent. Based on this test, the inheritance of leaf rust resistance in Wampum best fit a simple additive genetic model with no dominance or epistatic interactions. Resistance in Wared fit an additive-dominance model with no epistatic interaction, whereas the resistance in Borah was best explained by a genetic model assuming significant additive X additive interaction. They observed that the resistance was additive in crosses between resistant cultivars and the nature of gene action was best explained by genetic models assuming significant interaction components. They did not find any differences between reciprocal F1 or F2 generations of any cross.

Bjarko and Line (1988b) also studied the heritability (both broad sense and narrow sense) and the number of genes controlling leaf rust resistance from the above mentioned experiment. They evaluated 100 F3 lines and 40-45 F5 lines per cross along with the parents. They did not find any discrete phenotypic classes in the segregating populations of any cross. Based on quantitative analyses they found that each resistant cultivar contained at least two to three genes for leaf rust resistance. Also each cultivar had different genes for resistance. When the narrow-sense heritability estimates were determined using the crosses between the susceptible cultivar Twin, and the cultivars Wared, Wampum, and Borah the values were 0.72 to 0.92, 0.42 to 0.70, and 0.33 to 0.55; respectively. Broad-sense heritability estimates were generally higher than the narrow-sense heritability estimates.

Inheritance of Latent Period

Kuhn et al. (1980) studied the inheritance of latent period of leaf rust in slow leaf rusting wheat. They evaluated 81 F3 families derived from the cross of the slow rusting cultivar Suwon 85 and the fast rusting cultivar Suwon 92. Distribution of F3 family mean latent period indicated partial dominance for short latent period, and gave little evidence for distinct classes. They classified the F3 families into F2 genotypes based on the family mean, range and apparent segregation. The resulting classification gave an acceptable fit to a two gene model.

The inheritance of latent period was also studied by Lee and Shaner (1985a). Crosses were made between six slow leaf rusting wheat cultivars: 'P6082', 'Suwon 85', 'L574-1', 'CI-10745', 'Milyang 8-6', 'SW72469-6' and two fast rusting cultivars 'Morocco' and 'Suwon 92'. Analyses of F3 families from crosses between slow and fast rusting cultivars and F1 backcrosses showed that the long latent period in slow rusting wheats was conditioned by two partially recessive genes with equal effects. In a subsequent study Lee and Shaner (1985b) observed transgressive segregation for length of latent period. When intercrossing six slow rusting wheat cultivars, the resulting segregating populations all showed transgressive segregation. Plants with latent periods shorter than either parent and as short as that of the susceptible check Morocco were observed. Other F2 plants had longer latent periods than either parent and as long as that of the slowest rusting cultivar. These results indicate that most of the genes conditioning long latent period in these six cultivars differ from each other and that they show additive effects.

Associations Among Components of Slow Rusting

The correlation between latent period and uredium size was studied by Kuhn et al. (1980) in the F_3 population derived from a cross between the slow leaf rusting cultivar Suwon 85 and fast leaf rusting cultivar Suwon 92. They observed a negative correlation ($r = -0.55$ to $r = -0.63$) between these components. Negative correlations between latent period and uredium size were also observed by Lee and Shaner (1985a) in the F_2 populations of crosses between slow and fast leaf rusting wheat cultivars. Singh et al.(1990) studied associations among various components of slow rusting using several CIMMYT-derived varieties/lines. They observed moderately high negative correlations of latent period with uredium size and receptivity and a strong positive correlation between uredia maturity and latent period.

Correlation Between Disease Development in the Field and Components of Slow Rusting

Shaner and Finney (1980) observed that leaf rust developed more slowly in the field on cultivars that showed longer latent period and smaller and fewer uredia in the greenhouse experiments. They reported a r value of -0.71 between area under the leaf rust progress curve (AULRPC) and latent period. Singh et al. (1990) also reported that wheat genotypes with a small AULRPC from field data had a longer latent period, smaller uredium size, and reduced receptivity in the greenhouse.

Slow Rusting Resistance to Stem Rust (Puccinia graminis f.sp.tritici) of Wheat

Slow rusting resistance to stem rust in wheat has a similar mode of resistance as leaf rust. A review article by Wilcoxson (1986) discusses different aspects of slow stem rusting in wheat. Only specific studies on the inheritance of slow rusting to stem rust will be cited here.

The inheritance of slow rusting to stem rust in wheat was studied by Skovmand et al.(1978). They used F5 progenies derived from a diallel cross of seven spring wheat cultivars. Two cultivars ('Baart' and 'Prelude') were fast rusting while the others ('Idaed 59', 'Lee', 'Kenya 58', and 'Thatcher') had different degrees of slow rusting. Slow rusting was estimated from the area under the disease progress curve. The distribution of the progenies in each cross, except those involving Kenya 58 and Idaed 59, resembled normal distribution. Transgressive segregation for slow rusting occurred in each cross. The genetic control of slow rusting was predominantly additive though epistatic gene action was also detected. Narrow-sense heritability, estimated from the variance components of the diallel analysis was 82%. The number of segregating genes for slow rusting was estimated to be 2 to 12 pairs, depending on the cross.

Another study on the inheritance of slow rusting to stem rust of wheat was reported by Ayers et al.(1981). They studied slow rusting using F6 progenies of two crosses involving the slow rusting spring wheat line 'FKN' and two fast rusting lines, 'W3498' and '3-106'. They also used the area under the disease progress curve to measure the rate of rust development. Progenies in both crosses had a symmetrical distribution about the mean for slow rusting.

Broad-sense heritability estimates for slow rusting were 66 and 52% for FKN/W3498 and FKN/3-106 crosses respectively.

Knott and Padidam (1988) reported a study on the inheritance of stem rust resistance in six wheat lines having adult plant resistance. Crosses were made to a susceptible line and the progenies were advanced to the F5 generation by the single seed descent method. Depending on the crosses they tested 91 to 135 F5 derived F7 lines with race 15B-1 in the field. The number of genes controlling resistance was estimated by grouping the F7 lines of a cross into two classes: lines as resistant as the resistant parent in one class and all other lines in the other class. They tested the ratio of the lines in these classes against the ratios expected with various numbers of genes. They observed that for all six crosses, segregation ratios best fit either three- or four-gene models.

Inheritance of slow rusting in other crops

The inheritance of slow rusting has been studied in crops other than wheat. Several examples in other cereal crops and ryegrass are noted.

Johnson and Wilcoxson (1979) studied slow rusting resistance to barley leaf rust (Puccinia hordei) in nine crosses among fast and slow rusting barley genotypes and found that differences in the disease development were continuously distributed among the progenies with transgressive segregation being common. Estimates of heritability varied from 13 to 65%.

In a study of the inheritance of latent period in the barley to barley leaf rust, Parlevliet and Kuiper (1985) found that the barley cultivar 'Cebada Capa' had four to six minor genes controlling latent period. They obtained this result

from crossing Cebada Capa with a barley cultivar 'L94', which is assumed to carry no genes for increased latent period.

Inheritance of slow rusting in corn was studied by Kim and Brewbaker (1977) by means of diallel and generation mean analyses of crosses among 11 inbred corn lines in severe epidemics of Puccinia sorghi. The results of the diallel analysis indicated that the nine parents had significant general combining ability estimates for slow rusting. Heterosis was not found and specific combining ability estimates were small but significant. Generation mean analysis showed broad-sense and narrow-sense heritabilities of 83% and 47% respectively.

Luke et al. (1975) found a continuous distribution for slow rusting to oat crown rust among the progenies of crosses infected with Puccinia coronata. The nature of gene action indicated some partial dominance for fast rusting with a broad sense heritability estimate of 87%. Harder and McKenzie (1984) reported a complex additive-type of resistance to Puccinia coronata in wild oat (Avena sterilis).

Slow rusting resistance of ryegrass to Puccinia coronata f.sp. lolli was studied by Wilkins (1975) which included 12 parents. Ten parents appeared to have slow rusting response. He found that the genetic control of slow rusting was largely additive with a 22% of narrow-sense heritability estimate. He concluded that slow rusting was conditioned by a number of minor genes.

Artificial Inoculation

In studying disease resistance artificial inoculation is necessary to ensure an uniform epidemic and also to inoculate the host with the desired type of pathogen. Artificial inoculation of wheat plants with wheat rusts can be done in the field in different ways. Spreader rows can be used where plants of a highly susceptible cultivar are planted in between the experimental plots. This spreader row is then inoculated in the early tillering stage with the proper race by dusting the spores over the plants by means of a cyclone duster or by spraying the spore suspension with a sprayer. The spreader plants can also be inoculated by injecting spore suspension into the plants with a hypodermic syringe. Inoculation of experimental plants then take place from spore showers from the spreader plants. Experimental plants can also be inoculated directly by dusting or spraying the spores or by using a hypodermic syringe.

Ohm and Shaner (1976) inoculated wheat plants in both field and greenhouse studies by applying an aqueous spore suspension (with surfactant) of leaf rust to the foliage in studying slow rusting of wheat to leaf rust. Shaner and Finney (1980) assessed slow rusting resistance of winter wheat to leaf rust in hill plots. They inoculated three tillers in each hill by injecting an aqueous suspension of urediniospores of leaf rust into the leaf whorls with a hypodermic syringe.

In studying partial resistance of wheat to leaf rust, Parlevliet (1987) used spreader plants grown in pots. These spreader plants represented a highly susceptible cultivar. Inoculation was carried out in the early tillering stage by dusting the spores over the plants. Just prior to the formation of urediosori, the

pots were placed within the experimental area and removed after 10 to 14 days. For some experimental plots he inoculated by spraying spore suspension over the whole experimental plot on evenings that seemed very conducive for infection. Both methods appeared satisfactory in creating a uniform epidemic.

Inoculation in greenhouse experiments can be done using a settling tower which spreads spores more uniformly on the experimental plants. Plants to be inoculated are placed around the tower. The tower shutter is left closed for 10 sec to collect spore clumps and then left open for 3 min to allow spores to settle on leaves (Kuhn et al. 1978).

It is apparent that slow rusting resistance in wheat has been known for many years (Hayes et al. 1925). However, very little interest on this form of resistance was expressed until the great epidemics of wheat stem rust in the U.S.A. during 1953 -1954 (Stakman and Harrer, 1957). During the last 20 years there has been an increased interest in slow rusting resistance with the realization that it might be a more stable form of resistance in comparison to complete resistance. There is some evidence that slow rusting resistance is relatively durable. However, the durability of resistance is best judged over time.

CHAPTER 1

INHERITANCE OF SLOW RUSTING RESISTANCE TO LEAF RUST IN WHEAT

ABSTRACT

The inheritance of slow rusting resistance to leaf rust (Puccinia recondita f.sp. tritici) was studied in F_6 families resulting from a diallel cross involving one fast rusting and five slow rusting wheat (Triticum aestivum (L.)) genotypes. Parents and progenies were evaluated in a replicated field trial under epidemics initiated by artificial inoculation. Area under the leaf rust progress curve (AULRPC) was used to measure rust severity over time. Differences in the AULRPC were observed among crosses and among progeny within crosses. Transgressive segregation toward greater susceptibility was observed. The distribution of the progeny was skewed toward resistance. Predominantly additive gene action for slow rusting was detected, but additive X additive epistasis was also present. Narrow-sense heritability varied from 23.4% to 92.8% depending on the cross. The number of genes controlling slow rusting varied from two to four depending on the parents used in the cross. The correlation between slow rusting and plant maturity was low and negative. No relationship of plant height with slow rusting was observed.

INTRODUCTION

The often short-lived nature of race-specific, hypersensitive type of resistance to leaf rust in wheat cultivars has created the necessity to search for more durable types of resistance. Slow rusting resistance of wheat has been reported to be a more durable type of resistance (Caldwell, 1968; Kuhn et al. 1978; Rajaram et al. 1984) and has been identified for leaf rust (Caldwell et al. 1970; Gavinlertvatana and Wilcoxson, 1978; Milus and Line, 1980; Rajaram et al. 1984; Bjarko and Line 1988a, 1988b). The inheritance of slow rusting resistance to leaf rust in wheat has been reported to be polygenic with moderately high narrow-sense heritability estimates (Gavinlertvatana and Wilcoxson, 1978). In contrast, Bjarko and Line (1988b) found that the inheritance of slow rusting was oligogenic with moderately high narrow-sense heritability estimates. Gene action for slow rusting resistance to leaf rust has been reported to be additive without any dominance interaction in one slow rusting wheat cultivar, while in another slow rusting cultivar the gene action was best explained by an additive X additive interaction (Bjarko and Line, 1988a). Slow rusting resistance to stem rust was estimated to be controlled by 2 to 12 genes with predominantly additive gene action (Skovmand et al. 1978). Ayers et al. (1981) did not estimate the number of genes but symmetric distribution of the progenies about the mean led them to conclude that slow rusting to stem rust was quantitatively inherited.

To exploit the advantages of more durable resistance offered by slow rusting, more information on the inheritance and nature of gene action is

necessary. Wheat cultivars derived from CIMMYT germplasm are grown over 50.7 million hectares worldwide (Dalrymple, 1986). In a global context, durable disease resistance and genetic diversity are of paramount importance in the breeding program of CIMMYT (Rajaram et al.1988). Slow leaf rusting wheat genotypes have been identified and utilized in CIMMYT breeding program, however a genetic analysis of these slow rusting genotypes have not been conducted. A knowledge of the nature of inheritance of these valuable genotypes would increase their efficient use in the breeding program and thereby offer durability in future cultivars.

The objectives of this study were to determine: 1) the nature of inheritance and gene action of slow rusting resistance to leaf rust in wheat and 2) the relationships of slow rusting with cultivar maturity and plant height.

MATERIALS AND METHODS

Parental materials involved in this study were six spring wheat genotypes: 'Yecora 70', 'Sonoita 81', 'Tanager'S', 'Galvez 87', 'Ures 81', and 'Moncho'S'. Yecora 70 is a fast rusting cultivar, while the remaining parents have different degrees of slow rusting (S. Rajaram, personal communication). Detailed pedigrees of the parental materials are presented in Appendix Table 1. These six parents were crossed in a diallel series and reciprocals were bulked. Crosses were made in the field in February 1986 at the Centro de Investigaciones Agricolas del Noroeste (CIANO) Experiment Station at Cd. Obregon, Mexico. F_1 seed was harvested in April 1986 and advanced through the F_3 generation by the single seed descent in the greenhouse at the Oregon State University campus, Corvallis, Oregon. F_4 and F_5 generations were grown in the field at CIANO, Cd. Obregon and the International Maize and Wheat Improvement Center (CIMMYT), El Batan, Mexico, in 1988 respectively. Fifty-four F_6 lines from each of the 15 crosses were used to study the inheritance of slow rusting. Seeds from a single F_5 plant was taken to form each F_6 line. The six parents and the progenies were planted in the field at Cd. Obregon on November 22, 1988 using a randomized complete block design with three replications. In addition, all six parents were included after every 200 entries in each replication as checks.

Each entry was hand-planted in a 1.5-m long single row plot. Seeds were spaced an average of 5 cm apart in the plots. One row of CIANO 79, a spring wheat cultivar, which is highly resistant to the known leaf rust races in the Yaqui

valley of Mexico, was planted between adjacent plots to reduce movement of spores among entries. The distance between rows was 30 cm. The blocks were divided into subblocks for the purpose of irrigation. Each subblock accomodated 152 plots. These 152 plots were planted in four strips with 1 m between strips. Borders of CIANO 79 were also planted horizontally between adjacent strips in the middle of this 1m space, leaving a 0.5 m alley along each strip. Fertilizer was applied at the time of land preparation at the rate of 150 Kg/ha of nitrogen, and 80 Kg/ha of phosphorous. Nitrogen fertilizer at the rate of 50 Kg/ha was top-dressed at the early tillering stage. Irrigation was applied as necessary to germinate seeds and to maintain good plant growth and rust development throughout the growing season.

Inoculation

The experimental plots were first inoculated with a single race of Puccinia recondita f. sp. tritici designated as MCD/SM [avirulence/ virulence formula: Lr2a, 2b, 2c, 3ka, 9, 11, 16, 18, 19, 21, 23, 24, 25, 29, 30, 32, 33/Lr1, 3, 3bg, 10, 13, 14a, 14b, 15, 17, 20, 26, 27+31, 28; Long and Kolmer (1989) and R.P.Singh of CIMMYT (personal communication)]. This race is virulent on seedlings of all parental materials used in this study. Tests for virulence were conducted on seedlings in the greenhouse at CIMMYT by R.P. Singh. Inoculations were conducted as follows: Inoculum was suspended by mixing 250 mg of urediospores per liter of purified water and one drop of surfactant (Tween 20) were added to this suspension. Inoculation was done on

3 February, 1989 when the plants were at the stage when main shoot and eight or more tillers had developed (growth stage 28-29 of the Zadoks scale (Zadoks et al.1974). Four tillers from each end of each experimental unit were inoculated with the spore suspension using hypodermic needles. Uredia were observed on the terminal leaves from the inoculated tillers at 10-13 days after inoculation. However, heavy disease was not observed by 6 weeks post-inoculation. To ensure an epidemic, plots were inoculated on the evenings of March 8, 9, 14, and 15 by spraying a spore suspension made from fresh inoculum collected from spreader rows used in the CIMMYT bread wheat nursery. The suspension was prepared using urediospores at the rate of 0.025 mg/ml of water and two drops of Tween 20 per 5 liters of water. Inoculum was applied with a motorized backpack sprayer equipped with a 5 m boom carrying nozzles every 75 cm. The boom was held by two persons walking at a constant speed along the sides of the plots. Although the spray inoculations were done with a collection of inoculum from bread wheat program spreaders, later analysis of races from the bulk collections of inoculum from the experiment indicated that race MCD/SM predominated (R.P. Singh, personal communication).

Data Collection

Days to anthesis was recorded for each experimental unit on a plot basis as the number of days from the first irrigation after seeding to the time when 50% of the heads in a plot had flowered.

Rust severity was estimated for each plot at weekly intervals for three weeks using the modified Cobb scale (Peterson et al.1948 and Stubbs, et al.

1986). Each reading per replication was completed in one day. The first reading was taken begining 11 days after the last inoculation. Ten flag leaves were observed from the middle 60 cm of each plot and given an average severity value and the reaction type of the pustules (S = susceptible, MS = moderately susceptible, or MR = moderately resistant) per plot. The severity was recorded from the middle of the plot to avoid the high disease pressure created on the plants at the ends of the plots previously inoculated with hypodermic needles.

Plant height was measured on a plot basis at maturity from the ground level to the top of the spike and was based on a single measurement.

Statistical and Genetic Analysis

Area under the leaf rust progress curve (AULRPC) for each experimental unit was calculated from the weekly rust severity estimates using a computer program developed at CIMMYT. This program calculates AULRPC using the following formula:

$$AULRPC = \Sigma (x_i + x_{i+1})/2)t_i$$

where, x_i = rust intensity on date i, t_i = time in days between date i and date i+1, and n = number of dates on which disease was recorded.

The AULRPC-value of a line measures the severity as well as the rate of disease development for that line and represents the relative slow rusting characteristics of a genotype.

Analysis of variance was computed on the AULRPC-values for each cross separately and combined for all crosses. General combining ability (GCA) and specific combining ability (SCA) variances were computed according to the

model II, method IV of Griffing (1956). Model II is a random effects model, and method IV includes only one set of F_6 families from the diallel cross and excludes the reciprocals and the parents.

Gene action was estimated from the variance components of general and specific combining ability using the method of Horner et al. (1955). The combining ability variances were then expressed in terms of covariance of full sibs (cov_{FS}) and covariance of half sibs (cov_{HS}). The additive and non-additive genetic variances were estimated from GCA and SCA variances as follows:

$\sigma^2_g = cov_{HS}$

$\sigma^2_s = cov_{FS} - 2(cov_{FS} - cov_{HS})$

$Cov_{HS} = [(1 + F)/4]\ \sigma^2_A + [(1 + F)/4]^2\sigma^2_{AA}$

$Cov_{FS} = [(1 + F)/2]\sigma^2_A + [(1 + F)/2]^2\sigma^2_D + [(1 + F)/2]^2\sigma^2_{AA}$

where,

F = inbreeding coefficient of the parents, which is 1 in this study because the parents were completely inbred.

σ^2_g = variance component of GCA

σ^2_s = variance component of SCA

σ^2_A = additive genetic variance

σ^2_{AA} = additive X additive genetic variance

σ^2_D = dominance genetic variance

Therefore,

$\sigma^2_g = cov_{HS} = 1/2\ \sigma^2_A + 1/4\ \sigma^2_{AA}$, and

$\sigma^2_s = \sigma^2_A + \sigma^2_D + \sigma^2_{AA} - 2(1/2\sigma^2_A + 1/4\ \sigma^2_{AA})$

$= \sigma^2_D + 1/2\ \sigma^2_{AA}$

In this study variance associated with dominant-type gene action can be considered negligible due to the level of inbreeding of the progenies (F_6). Thus,

$\sigma^2_s = 1/2\ \sigma^2_{AA}$

or, $\sigma^2_{AA} = 2\ \sigma^2_s$

and $\sigma^2_A = 2\ \sigma^2_g - \sigma^2_s$

Heritability in the narrow sense was calculated from the diallel analysis estimates of genetic variances using the formula: $h^2_n = \sigma^2_A/\sigma^2_p$

Narrow-sense heritability for each cross was estimated using the following formula:

$$h^2_n = \sigma^2_g/\ \sigma^2_p;$$

σ^2_g and σ^2_p were estimated from the ANOVA table of each cross as follows:

$\sigma^2_g = (\sigma^2L - \sigma^2_E)/r$, and $\sigma^2_p = \sigma^2_g + \sigma^2_E$

Where, h^2_n = heritability estimate in narrow sense; σ^2_g = genetic variance; σ^2_L = variance among the F6 lines, which is obtained from the treatment mean square, σ^2_E = error variance, and r = number of replications.

The number of genes controlling slow rusting in each of the slow rusting parents was estimated using the method of Wright (1968) with some modification for the level of inbreeding of the progenies (F_6) as follows:

$$N = R^2/(\sigma^2_g \times 4.27)$$

where, N = number of genes, σ^2_g = genetic variance among F_6 families, R = estimated genotypic range.

R was measured by three methods:

(i) R = Phenotypic range of the parents

(ii) R = Phenotypic range of the progenies

(iii) R = Phenotypic range of the progenies X heritability in the particular cross. In the first two methods phenotypic range is considered as the genotypic range, while in the third method the environmental influence is accounted for and thus gives a better estimate of the genotypic range (Multize and Baker, 1985).

The relationship of slow rusting with plant maturity and plant height was examined by phenotypic mean correlations of AULRPC with days to anthesis and plant height.

RESULTS AND DISCUSSION

All of the parents showed a susceptible reaction type in the field (either S or MS). Most of the progeny had either S or MS type reactions with very few having MR type reactions to the leaf rust races used. The seedling and adult plant infection types for the parents observed in the greenhouse with the leaf rust race MCD/SM is presented in Table 1.1. All of the parents had susceptible reaction types both at seedling and adult plant stages (Infection type 3 to 4).

Of the six parents, the fast rusting parent Yecora 70 had the highest mean AULRPC (871.5), while the mean AULRPC for the five slow rusting parents varied from 6.25 for Galvez 87 to 54.75 for Ures 81 (Table 1.2). Large variations in the mean AULRPC were observed among the crosses (Table 1.3). Crosses involving a fast and a slow rusting parent had higher AULRPCs than the crosses involving only slow rusting parents, except one cross (Yecora 70 X Sonoita 81), which had a lower value than the crosses between slow rusting parents.

There was rust present prior to the spray inoculations. The race used for first inoculation (by injection) predominanted the rust population in the experiment, therefore, this inoculation probably had the dominant influence. There was opportunity for disease to progress considerably from the first disease assessment (11 days after the last inoculation) until the final assessment (25 days after the last inoculation)(Figure 1.1).

For no cross was the frequency distributions of the F_6 lines for AULRPC normally distributed (Figures 1.2 to 1.16). Progeny of four crosses showed a continuous distribution while progeny of the remaining crosses had discrete distributions. The distributions of the progeny were skewed toward resistance in all crosses. From the mean AULRPC of the parents, the range of the F_6 family lines, and the frequency distribution of the prognies it can be observed that transgressive segregation toward greater resistance and susceptibility occurred in each of the crosses (Tables 1.2 and 1.3 and Figures 1.2 to 1.16). However, significant ($LSD_{.05}$) transgressive segregation was found only for greater susceptibility. Transgressive segregation suggests that the genes for slow rusting in the slow rusting parents are different.

Heritability and Gene Action

Analysis of variance for AULRPC showed differences among crosses, lines and replicates (Table 1.4). Differences among lines within each cross were also observed. Crosses between fast and slow rusting parents gave higher narrow-sense heritability estimates than the crosses between slow rusting parents (Table 1.5). The highest (92.8%) and the lowest (23.4%) heritability values were observed in the crosses Yecora 70 X Moncho'S' and Tanager'S' X Moncho'S', respectively. Among all of the crosses involving only slow rusting parents, the cross Galvez 87 X Moncho'S' had the highest narrow-sense heritability estimate (78.1%). When heritability in the narrow sense was estimated using the genetic variance components estimated from GCA and SCA variance components a value of 63.3% was observed. Similar narrow-sense heritability

estimates for slow leaf rusting have also been reported by other authors (Gavinlertvatana and Wilcoxson 1978; Bjarko and Line 1988b).

Both general and specific combining ability variances were significant (Table 1.6). The ratio of GCA to SCA was high, suggesting that additive genetic variance played a greater role than non-additive genetic variance in the expression of slow rusting resistance as measured by the AULRPC in the genotypes evaluated. The genetic components of variances (σ^2_A and σ^2_{AA}) estimated from GCA and SCA variance components are presented in Table 1.7. The estimate of the additive X additive genetic variance (σ^2_{AA}) was almost half of the additive genetic variance (σ^2_A) estimate. This indicates that, although additive genetic variance is predominant, additive X additive epistasis also plays a role in slow leaf rusting resistance in wheat. However, both additive and additive X additive genetic effects can be utilized in self-fertilizing crops. Our results suggesting a predominance of additive gene action are in agreement with the findings of Bjarko and Line (1988a) for slow rusting resistance to leaf rust in wheat and Skovmand et al. (1978) for slow rusting resistance to stem rust in wheat.

Estimates of Number of Genes

The three methods used to estimate the number of genes assumed that there is no linkage, no epistasis, no dominance, all loci have equal effects. In addition, the first method also assumed that all the alleles segregating for slow rusting resistance are in a single parent of the cross. When phenotypic range of parents were considered as genotypic range, the estimates of number of genes

and Moncho'S,' respectively (Table 1.8). When phenotypic ranges of the progeny lines were used as the genotypic range, the number of genes estimated were 6.0, 2.4, 2.8, 2.4, and 2.3 for Sonoita 81, Tanager'S', Galvez 87, Ures 81, and Moncho'S', respectively. When the phenotypic ranges of the progeny lines accounted for environmental influence (multiplying the range by the heritability of the cross) were used, the number of genes estimated were 4.4, 1.8, 2.2, 1.7, and 2.0 for the parents Sonoita 81, Tanager'S', Galvez 87, Ures 81, and Moncho'S,' respectively.

The method using parental difference as a measure of genotypic range often underestimates the number of genes, while the method using phenotypic difference of the progeny lines as genotypic range tends to overestimate the number of genes (Bjarko and Line, 1988b). Therefore, an average of the number of genes estimated in these two methods was determined (Table 1.8). According to Mulitze and Baker (1985) the method using the phenotypic range of the progeny lines accounted for environmental influence gives a better estimate of genotypic range. The average of the number of genes estimated by the first two methods corresponds closely to the third method (Table 1.8) and suggests that Sonoita 81 has 4 genes and each of the other four slow rusting parents have 2 genes for slow rusting resistance to leaf rust. Our results are in agreement with the findings of Bjarko and Line (1988b), who observed that two-to-three genes were involved in slow leaf rusting resistance in wheat. However, Gavinlertvatana and Wilcoxson (1978) suggested that 3 to 21 genes were involved in slow leaf rusting. Working with spring wheat genotypes Skovmand et

al. (1978) found that 2 to 12 genes were controlling slow rusting resistance to stem rust.

We conclude that selection for slow rusting resistance would be possible in early segregating generations of crosses involving these parents since only two-to-four genes are involved.

Associations of Slow Rusting with Plant Maturity and Plant Height

Significant variation among crosses and among lines for plant maturity was found. When the data combined over all crosses were considered, the correlation between the area under the leaf rust progress curve and plant maturity was negative and significant, but the coefficient of determination (R^2) was only 0.04. When individual cross data were analyzed, three of the 15 crosses had negative and significant correlations between maturity and area under the leaf rust progress curve (Table 1.9). However, the correlation values were low, except for the cross Ures 81 X Moncho'S' ($r = -0.48$). Considering the coefficient of determination, only 23.3% of the total variation in area under the leaf rust progress curve was explained by the difference in plant maturity in this particular cross. Therefore, slow leaf rusting in these crosses is not influenced by plant maturity. Selection for slow rusting genotypes combined with desired maturity should be successful. Our results are in agreement with the findings of Skovmand et al. (1978) who also reported a low and negative relationship of plant maturity and slow stem rusting in wheat.

The analyses of variance indicated significant variation for plant height among crosses and among lines within crosses. The correlation based on the

The analyses of variance indicated significant variation for plant height among crosses and among lines within crosses. The correlation based on the combined data for all the crosses was negligible (r = 0.02). However, when data from individual crosses were analyzed, four crosses had positive and significant correlations between plant height and area under the leaf rust progress curve, but the values were low (Table 1.9). The highest correlation coefficient value (r = 0.35) was found for the cross Yecora 70 X Ures 81. Only 11.9% of the total variation in area under the leaf rust progress curve is explained by the variation in plant height in this particular cross. Therefore, plant height has a negligible effect on slow leaf rusting.

Slow leaf rusting in these populations is controlled by two-to-four genes showing relatively high narrow-sense heritability. The gene action was predominantly additive, but additive X additive epistasis was also important. Based on this information it can be concluded that early generation selection for slow leaf rusting resistance in these crosses should be effective. Neither plant maturity nor plant height have a significant effect on the expression of slow rusting.

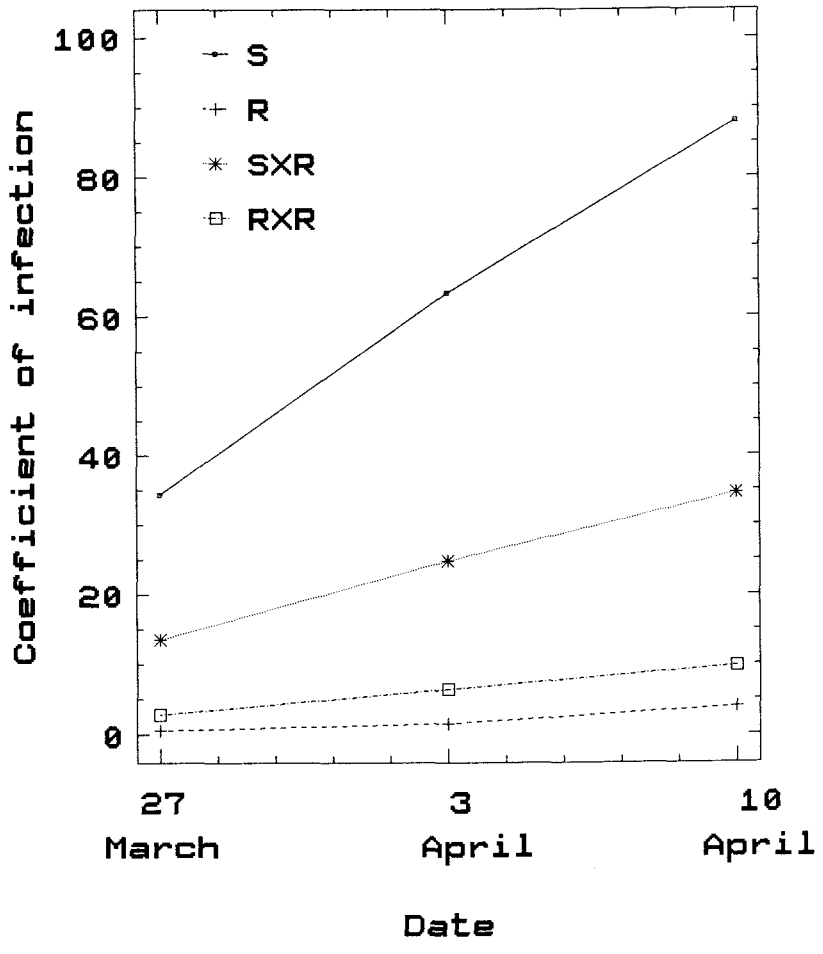

Fig.1.1. Disease severity over time for the susceptible parent Yecora 70 (S), the mean of the slow rusting parents (R), the mean of the progenies of all crosses between susceptible and slow rusting parents (SXR), and the mean of the progenies of all crosses between slow rusting parents (RXR).

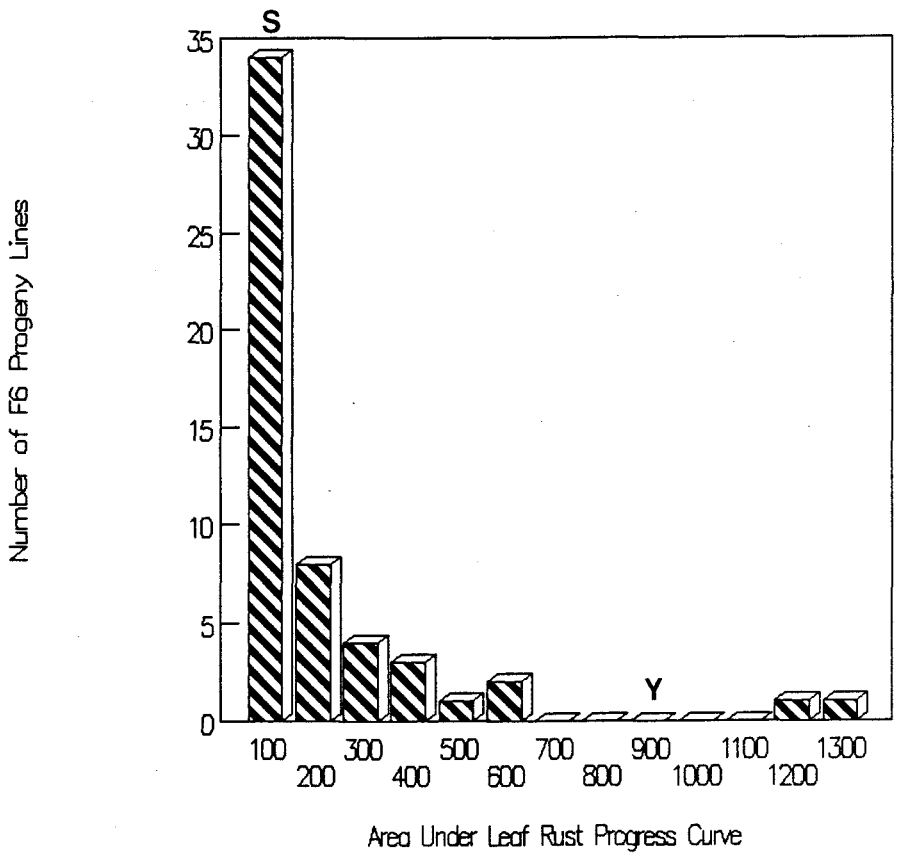

Fig.1.2. Frequency distribution for area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO in 1988-89. Parents (S = Sonoita 81, Y = Yecora 70) are indicated above the class in which they fall.

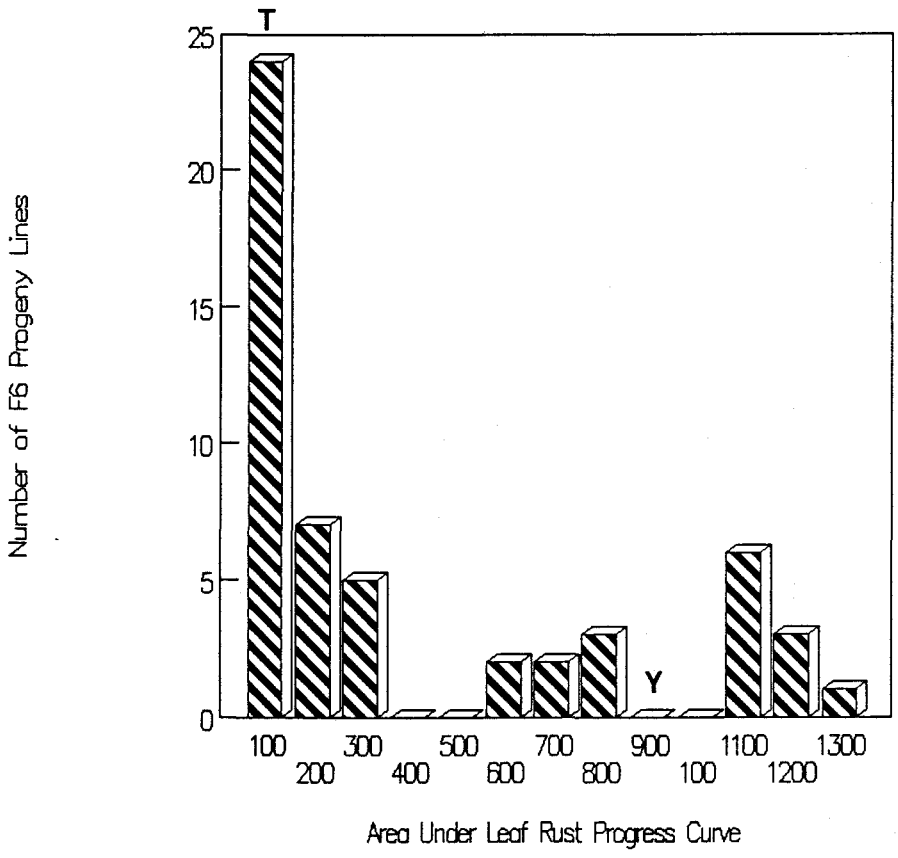

Fig.1.3. Frequency distribution for area under leaf rust progress curve of F_6 of wheat infected with leaf rust in the field at CIANO, 1988-89. Parents (T = Tanager'S', Y = Yecora 70) are indicated above the class in which they fall.

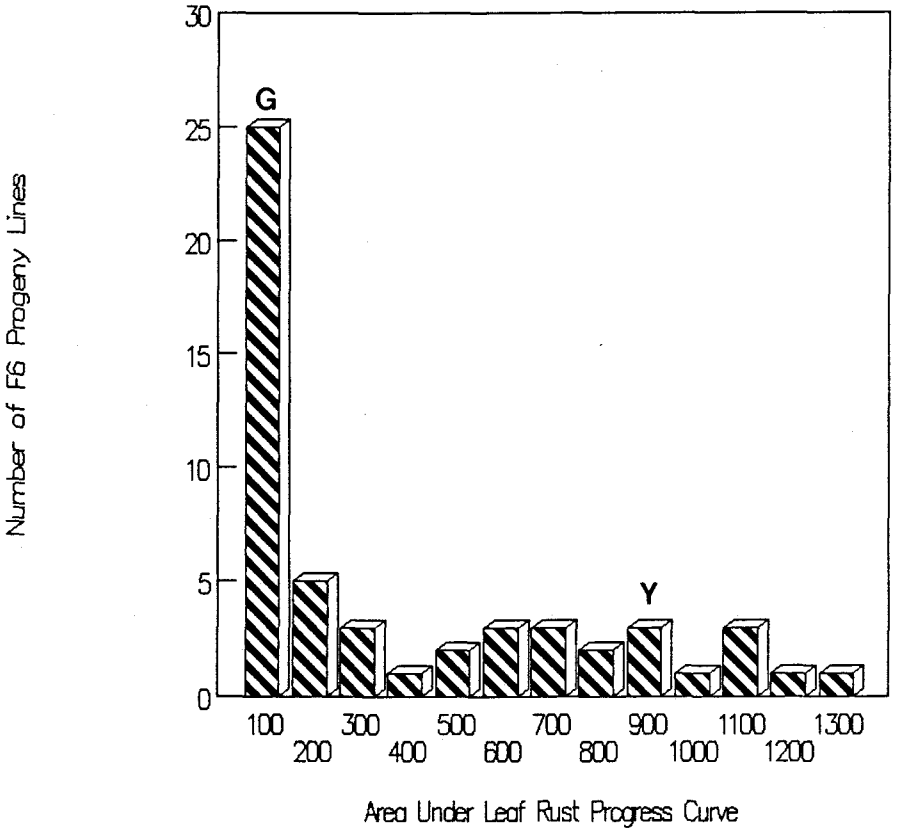

Fig.1.4. Frequency distribution for area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO in 1988-89. Parents (G = Galvez 87, Y = Yecora 70) are indicated above the class in which the fall.

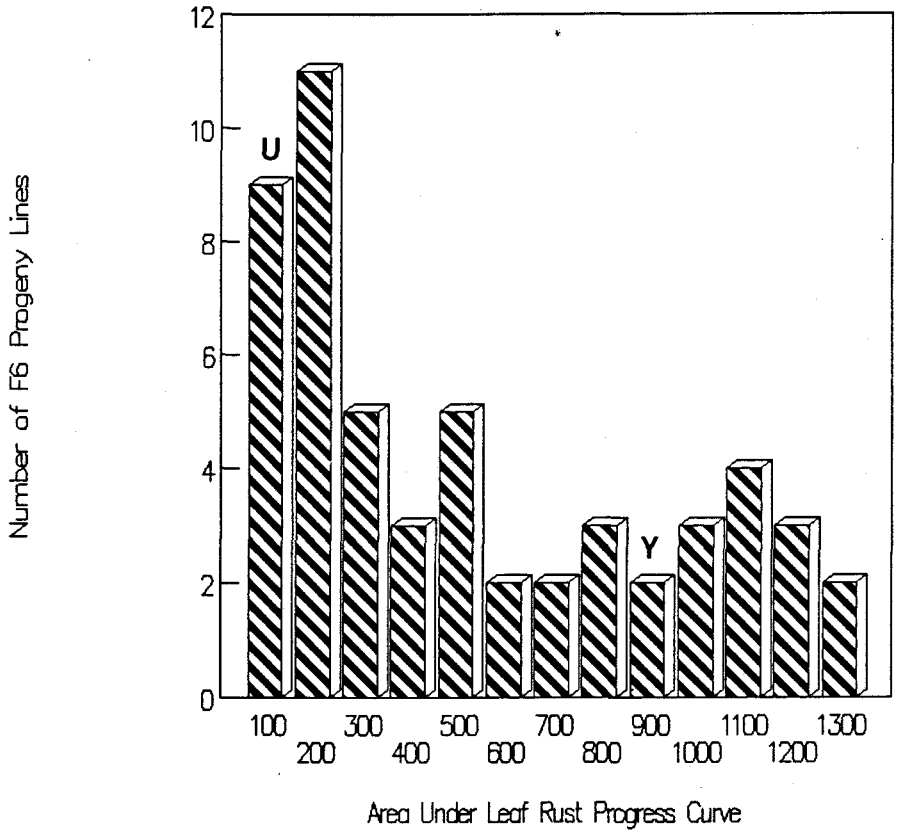

Fig.1.5. Frequency distribution for area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO, in 1988-89. Parents (U = Ures 81, Y = Yecora 70) are indicated above the class in which they fall.

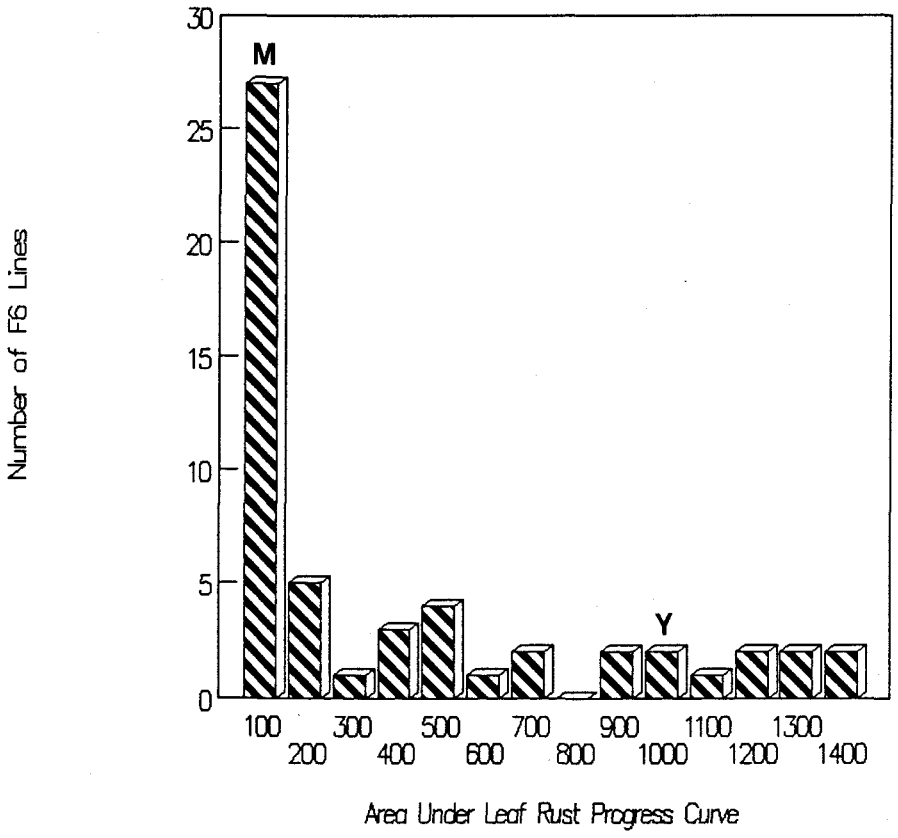

Fig.1.6. Frequency distribution for area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO, in 1988-89. Parents (M = Moncho'S', Y = Yecora 70) are indicated above the class in which they fall.

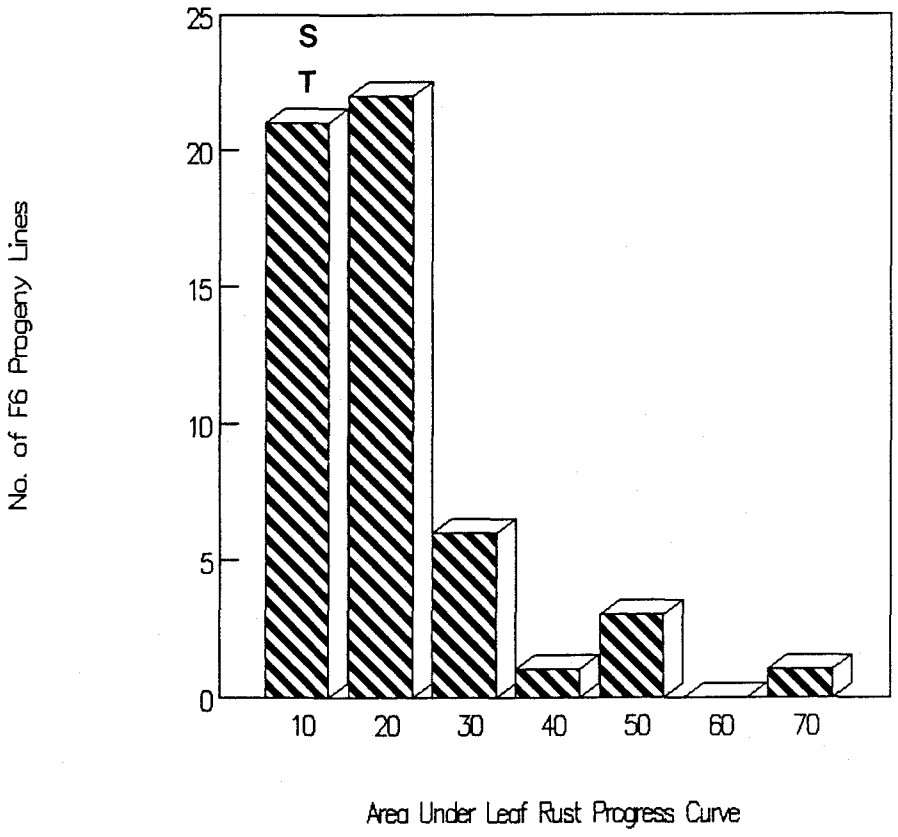

Fig.1.7. Frequency distribution for area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO, in 1988-89. Parents (S = Sonoita 81, T = Tanager'S') are indicated above the class in which they fall.

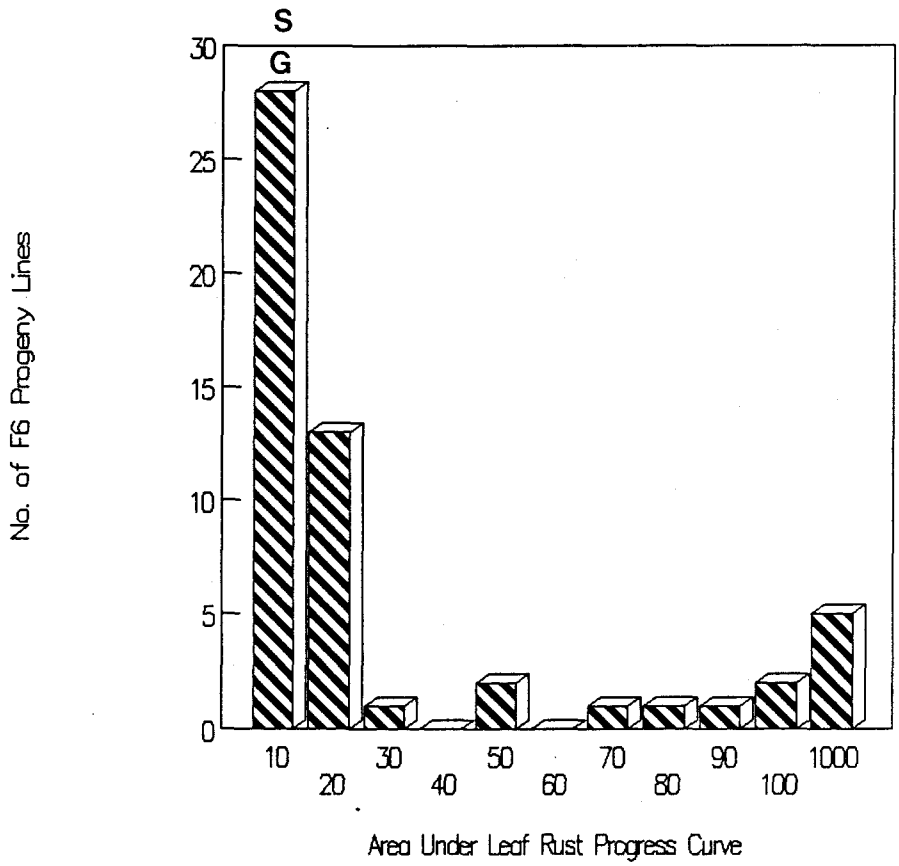

Fig.1.8. Frequency distribution for area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO, 1988-89. Parents (S = Sonoita 81, G = Galvez 87) are indicated above the class in which they fall.

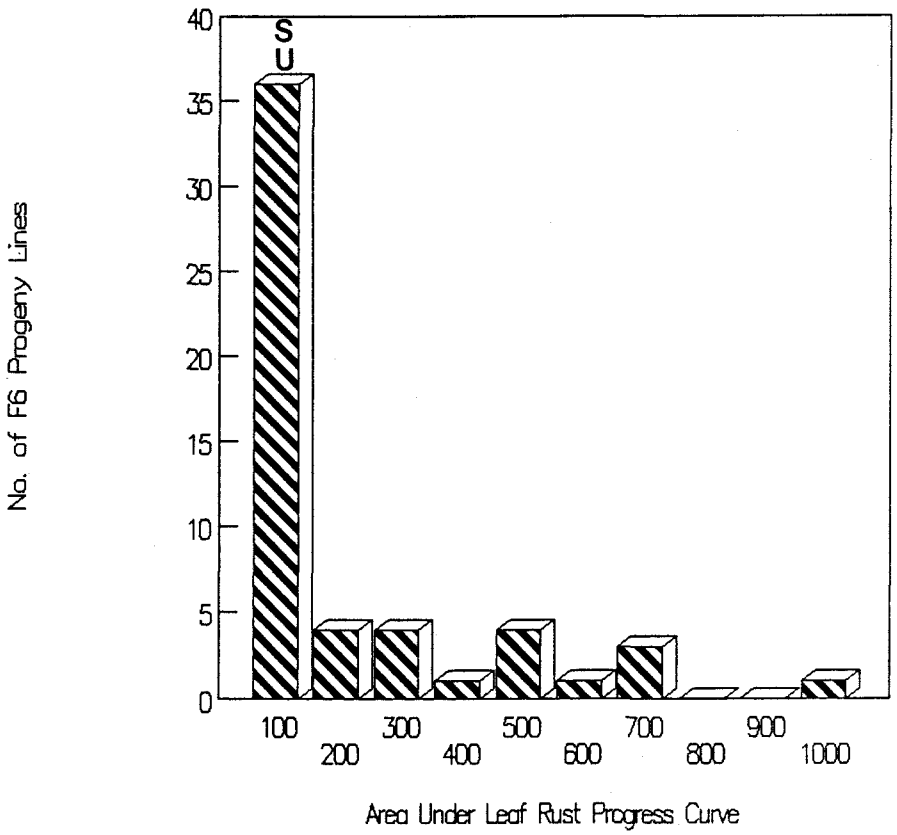

Fig.1.9. Frequency distribution for area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO, 1988-89. Parents (S = Sonoita 81, U = Ures 81) are indicated above the class in which they fall.

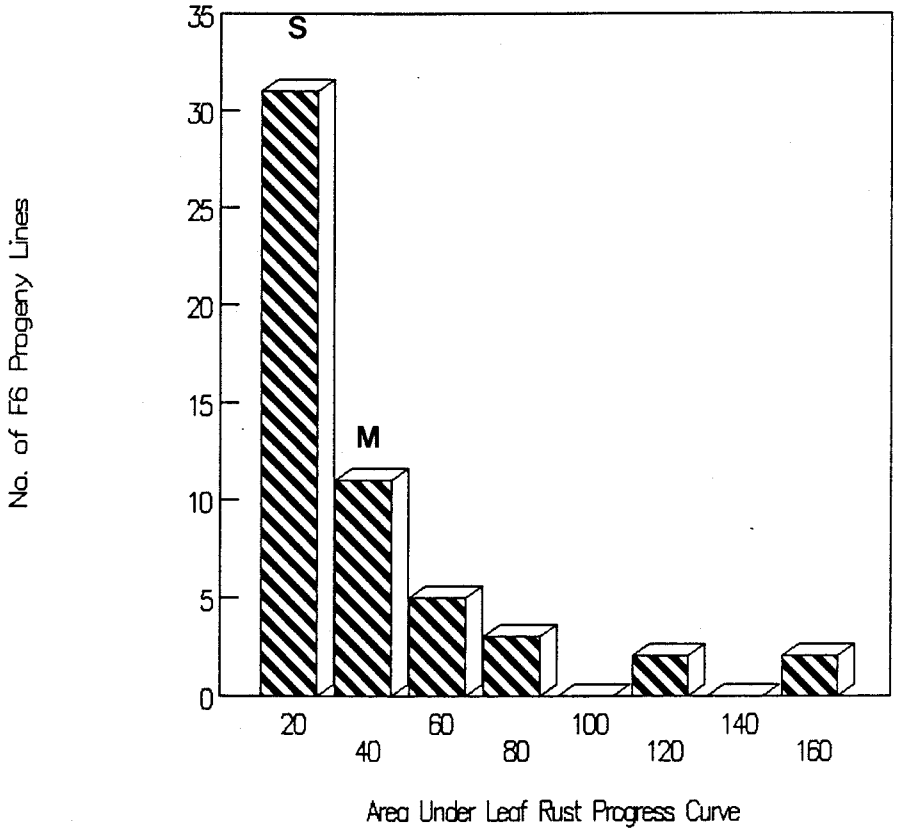

Fig.1.10. Frequency distribution for area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO, 1988-89. Parents (S = Sonoita 81, M = Moncho'S') are indicated above the class in which they fall.

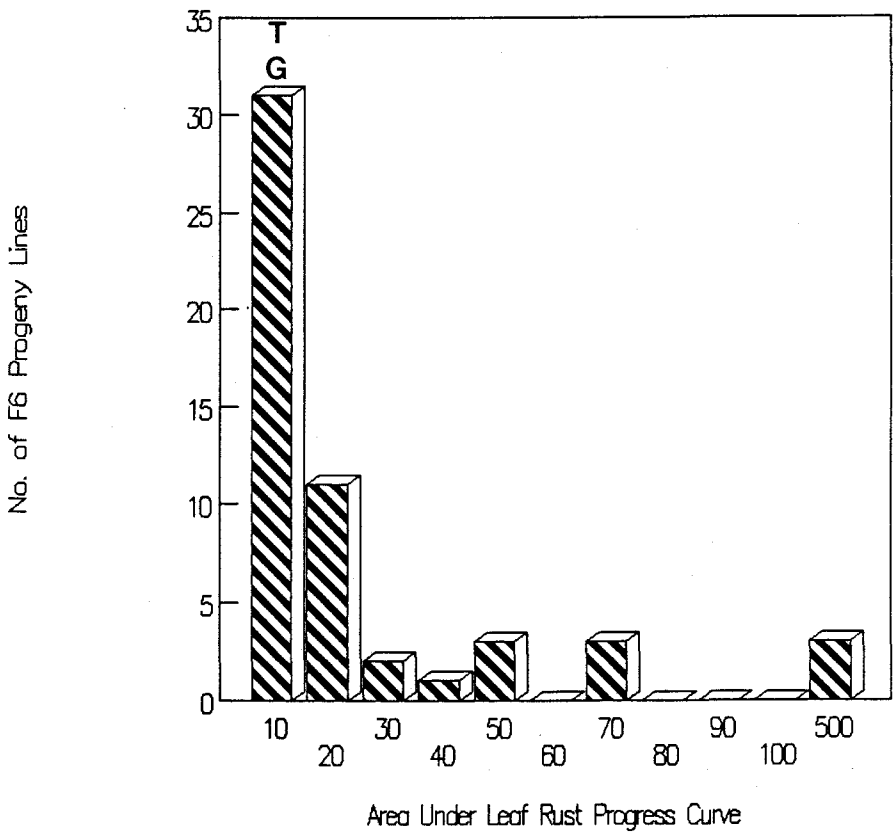

Fig.1.11. Frequency distribution for area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO, 1988-89. Parents (T = Tanager'S', G = Galvez 87) are indicated above the class in which they fall.

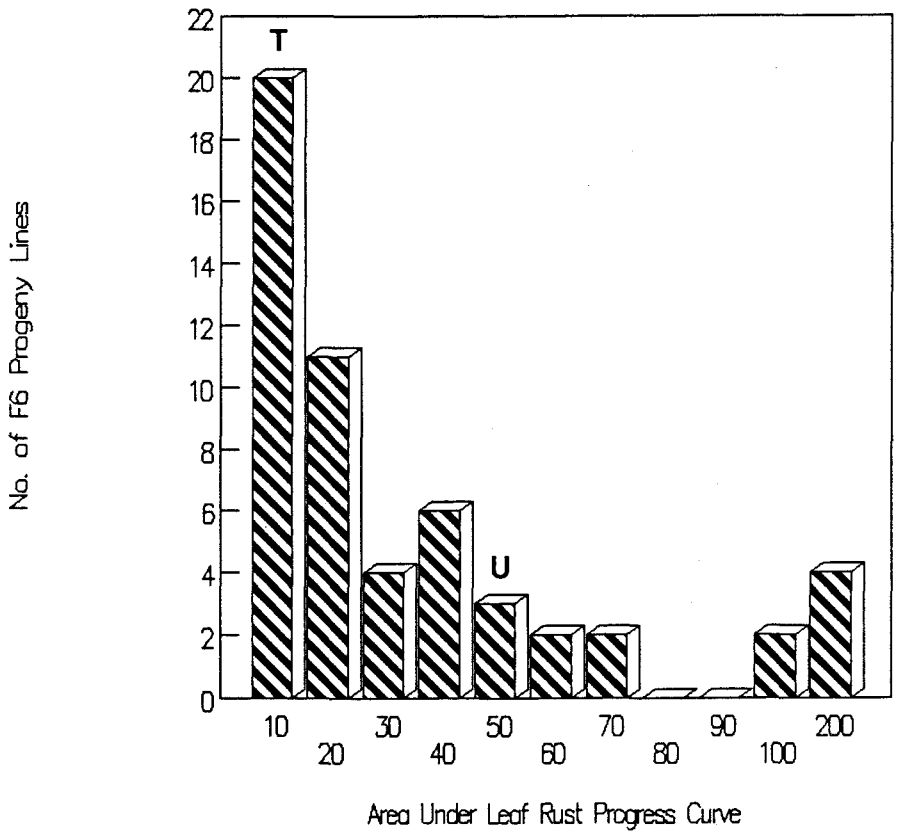

Fig.1.12. Frequency distribution for area under leaf rust progress curve of F_8 lines of wheat infected with leaf rust in the field at CIANO, 1988-89. Parents (T = Tanager'S', U = Ures 81) are indicated above the class in which they fall.

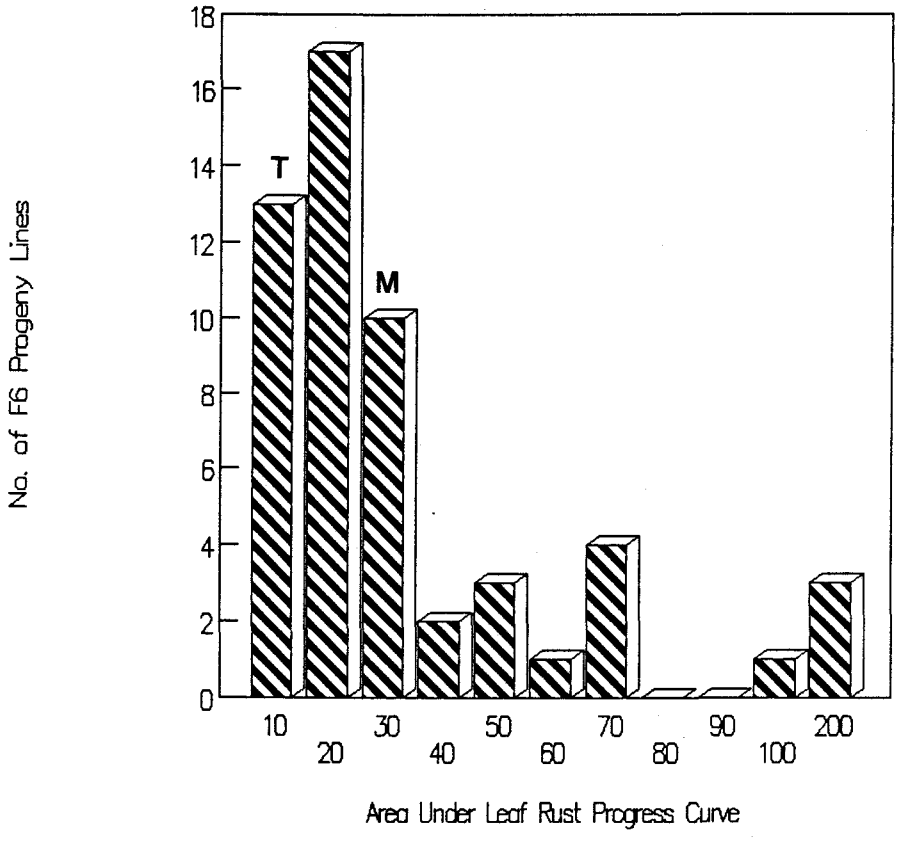

Fig.1.13. Frequency distribution of area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO in 1988-89. Parents (T = Tanager'S', M = Moncho'S') are indicated above the class in which they fall.

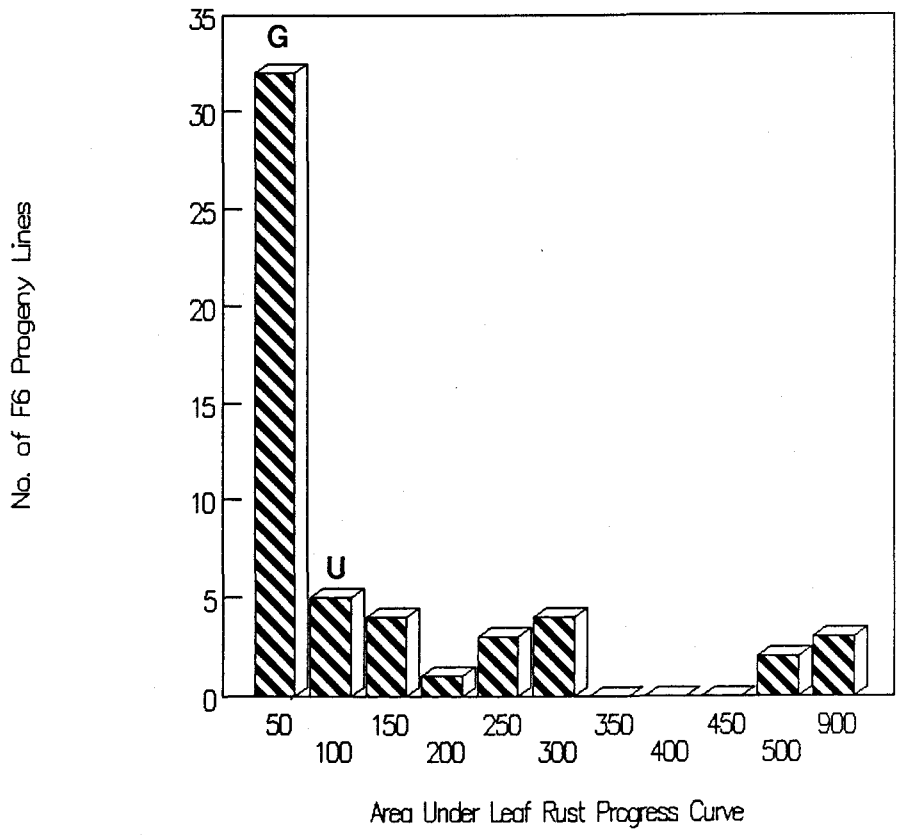

Fig.1.14. Frequency distribution for area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO in 1988-89. Parents (U = Ures 81, G = Galvez 87) are indicated above the class in which they fall.

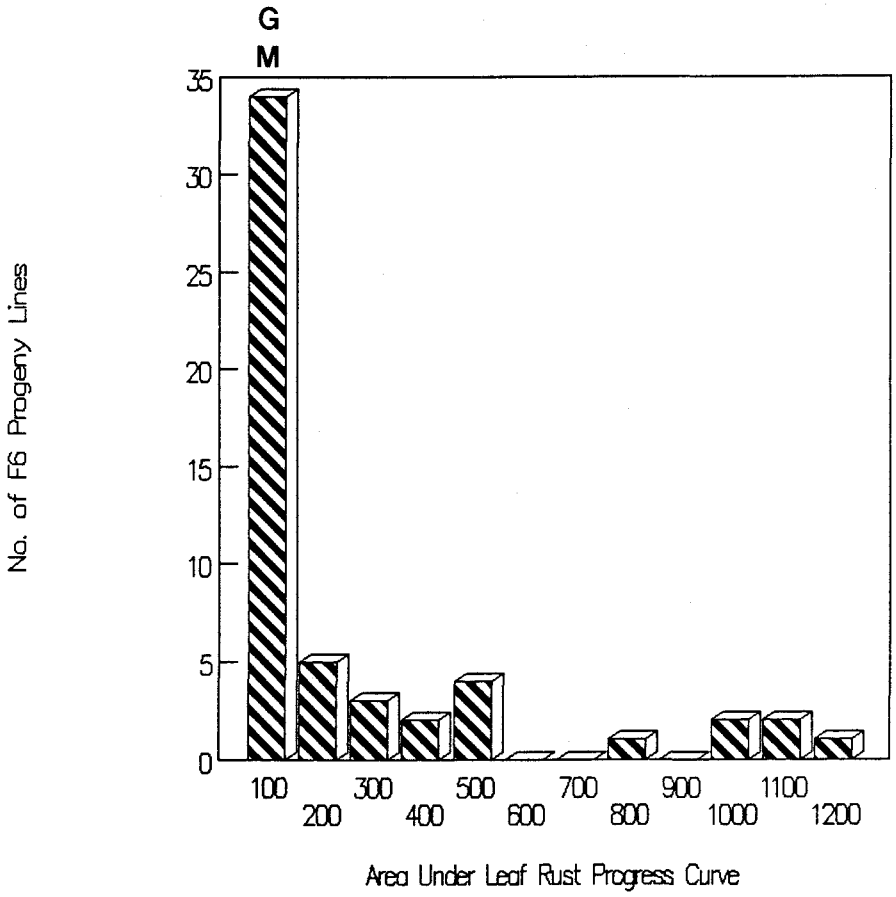

Fig.1.15. Frequency distribution for area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO, 1988-89. Parents (G = Galvez 87, M = Moncho'S') are indicated above the class in which they fall.

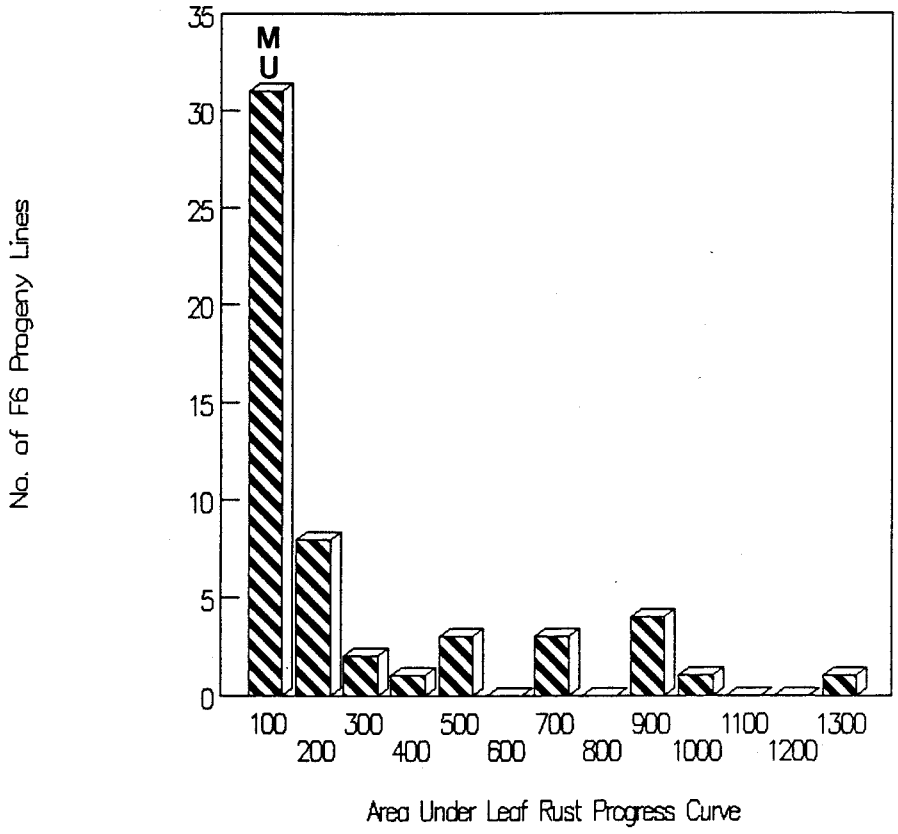

Fig.1.16. Frequency distribution for area under leaf rust progress curve of F_6 lines of wheat infected with leaf rust in the field at CIANO in 1988-89. Parents (U = Ures 81, M = Moncho'S') are indicated above the class in which they fall.

Table 1.1. Seedling and adult plant reaction of the six wheat cultivars/lines used as parents in the diallel cross, infected with leaf rust race MCD/SM in the greenhouse

Cultivars/Lines	Seedling reaction	Adult plant reaction
Yecora 70	4	4
Sonoita 81	3	3
Tanager'S'	3	3
Galvez 87	3	3
Ures 81	3	3^{+}
Moncho'S'	3	3

Table 1.2. Mean*, standard error (S.E.), and range of area under the leaf rust progress curve (AULRPC) for the six wheat cultivars/lines used as parents in the diallel cross grown at the CIANO field laboratory in 1988-89

Cultivars/lines	Mean ± S.E.	Range
Yecora 70	871.50 ± 47.06	644.0 - 1260.0
Sonoita 81	11.01 ± 0.19	8.4 - 11.2
Tanager 'S'	9.80 ± 1.47	0.0 - 22.4
Galvez 87	6.25 ± 1.21	0.0 - 11.2
Ures 81	54.75 ± 6.88	11.2 - 90.3
Moncho 'S'	29.38 ± 3.98	11.2 - 58.8

*, Mean of 15 observations, except for Ures 81, where one observation was missing.
$LSD_{(.05)}$ = 28.64

Table 1.3. Mean, standard error (S.E.), and range for area under the leaf rust progress curve (AULRPC) in the F_6 generation of 15 crosses derived from one fast rusting and five slow leaf rusting wheat cultivars/lines grown in the CIANO field laboratory, 1988-89

Cross	Mean ± S.E.	Range
Yecora 70 X Sonoita 81	151.63 ± 34.11	1.87 - 1236.67
Yecora 70 X Tanager'S'	372.91 ± 60.02	0.90 - 1376.70
Yecora 70 X Galvez 87	350.80 ± 54.52	0.00 - 1353.30
Yecora 70 X Ures 81	486.76 ± 53.08	14.00 - 1225.00
Yecora 70 X Moncho'S'	347.72 ± 58.76	10.27 - 1353.33
Sonoita 81 X Tanager'S'	13.97 ± 1.64	0.00 - 64.63
Sonoita 81 X Galvez 87	64.77 ± 22.40	0.00 - 924.00
Sonoita 81 X Ures 81	146.33 ± 29.32	2.33 - 915.83
Sonoita 81 X Moncho'S'	29.52 ± 4.61	0.93 - 145.13
Tanager'S' X Galvez 87	31.96 ± 10.98	0.00 - 446.83
Tanager'S' X Ures 81	30.67 ± 4.92	0.00 - 154.47
Tanager'S' X Moncho'S'	30.22 ± 4.87	0.00 - 173.13
Galvez 87 X Ures 81	119.79 ± 25.97	2.3 - 892.50
Galvez 87 X Moncho'S'	196.67 ± 42.99	0.00 - 1184.20
Ures 81 X Moncho'S'	224.08 ± 42.80	0.00 - 1283.30

Table 1.4. Analysis of variance for area under the leaf rust progress curve showing the combined analysis for 15 wheat crosses infected with leaf rust in the field at CIANO, 1988-89

Source	DF	Mean square
Reps	2	750418.2**
Crosses	14	3770442.9**
Progenies in crosses	795	215188.1**
Error	1618	13918.7

**, significant at P>.01

Table 1.5. Estimates of heritability (narrow-sense) for area under the leaf rust progress curve in F_6 generation of 15 crosses grown at the CIANO field laboratory, 1988-89

Cross	Narrow-sense heritability (%)
Yecora 70 X Sonoita 81	85.5
Yecora 70 X Tanager'S'	86.7
Yecora 70 X Galvez 87	88.1
Yecora 70 X Ures 81	85.5
Yecora 70 X Moncho'S'	92.8
Sonoita 81 X Tanager'S'	58.1
Sonoita 81 X Galvez 87	69.6
Sonoita 81 X Ures 81	73.8
Sonoita 81 X Moncho'S'	27.6
Tanager'S' X Galvez 87	77.9
Tanager'S' X Ures 81	27.8
Tanager'S' X Moncho'S'	23.4
Galvez 87 X Ures 81	64.4
Galvez 87 X Moncho'S'	78.1
Ures 81 X Moncho'S'	77.8

Table 1.6. Observed mean squares for general combining ability (GCA) and specific combining ability (SCA) for AULRPC involving 15 crosses grown at the CIANO field laboratory, 1988-89

Source	DF	Mean squares
GCA	5	55226.38**
SCA	9	5523.62**
Error	28	349.42
GCA/SCA		10.00

**, significant at P<.01

Table 1.7. Estimates of genetic and error variance components for AULRPC from F6 progeny lines of a 6X6 diallel cross grown at the CIANO field laboratory in 1988-89

Variance components	Estimated values
σ^2_A	19677.18
σ^2_{AA}	10348.40
σ^2_e	349.42

Table 1.8. Estimates of number of genes controlling slow rusting resistance as measured by area under the leaf rust progress curve in five spring wheat cultivars/lines infected with leaf rust in the field at CIANO, 1988-89

Cross	Number of genes			
	Method I*	Method II*	Method III*	Average
Yecora 70 X Sonoita 81	2.9	6.0	4.4	4.4
Yecora 70 X Tanager'S'	0.9	2.4	1.8	1.7
Yecora 70 X Galvez 87	1.1	2.8	2.2	2.0
Yecora 70 X Ures 81	1.1	2.4	1.7	1.7
Yecora 70 X Moncho'S'	0.9	2.3	2.0	1.8

*, Method I, Method II, and Method III are on the basis of how R, the genotypic range have been measured (see materials and methods).

Table 1.9. Correlation coefficient (r) and coefficient of determination (R^2) of area under the leaf rust progress curve with plant maturity measured as days from planting to anthesis and plant height

Cross	Plant maturity		Plant height	
	r	R^2	r	R^2
Yecora 70 X Sonoita 81	-0.07	0.01	0.24	0.06
Yecora 70 X Tanager'S'	-0.28*	0.08	0.24	0.06
Yecora 70 X Galvez 87	-0.16	0.03	0.23	0.05
Yecora 70 X Ures 81	-0.25	0.06	0.35*	0.12
Yecora 70 X Moncho'S'	-0.25	0.06	0.02	0.00
Sonoita 81 X Tanager'S'	-0.21	0.04	0.27*	0.07
Sonoita 81 X Galvez 87	0.03	0.00	0.24	0.06
Sonoita 81 X Ures 81	-0.18	0.03	0.31*	0.09
Sonoita 81 X Moncho'S'	-0.13	0.02	0.22	0.05
Tanager'S' X Galvez 87	-0.00	0.00	0.10	0.01
Tanager'S' X Ures 81	0.04	0.00	-0.14	0.02
Tanager'S' X Moncho'S'	-0.21	0.05	-0.05	0.00
Galvez 87 X Ures 81	-0.29*	0.09	0.16	0.02
Galvez 87 X Moncho'S'	-0.15	0.02	0.28*	0.08
Ures 81 X Moncho'S'	-0.48**	0.23	0.13	0.02

* and **, significant at $P<0.05$ and $P<0.01$, respectively.
N = 54

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CHAPTER 2

INHERITANCE AND POSSIBLE ASSOCIATIONS OF THREE COMPONENTS OF SLOW RUSTING IN LEAF RUST OF WHEAT

ABSTRACT

Latent period, receptivity, and uredium size are three important components of slow rusting resistance in wheat (Triticum aestivum L.). To study the nature of inheritance and possible relationships among these components, forty F_6 lines, the two parents, and a susceptible check cultivar were inoculated with leaf rust (Puccinia recondita f.sp. tritici) and evaluated in a replicated greenhouse trial. The slow rusting parent 'Sonoita 81' had a 39% increased length of latent period, 81% reduced receptivity, and a 77% decreased uredium size when compared to the fast rusting parent 'Yecora 70'. The latent period of Yecora 70 was 13% longer than that of the susceptible check Morocco. The distribution of F6 family mean uredia size and latent period were continuous between slow rusting and fast rusting parents. However, the distribution for receptivity was discrete. Narrow-sense heritability estimates were 62.5%, 57.5%, and 47.1% for uredium size, latent period, and receptivity, respectively. Estimates of the number of genes were two or three for latent period, three or four for uredium size and receptivity. Genotypic and phenotypic correlations between the latent period and uredium size were high and negative. Intermediate and negative correlations were found between latent period and receptivity, while the correlation between uredium size and receptivity was low and positive. Area under the leaf rust progress curve (AULRPC) and final rust severity (FRS) obtained from a subsequent field study with common entries were negatively correlated with latent period and positively correlated with uredium size. Correlations of receptivity with both AULRPC and FRS were not significant.

These results suggest that genetic improvement for the components of slow rusting is possible by applying a direct selection pressure in early segregating generations. Since the components are favorably associated, selection for one component would indirectly select for the others in the desired direction. Slow rusting genotypes can be selected through component selection in the greenhouse and AULRPC or FRS in the field.

INTRODUCTION

Leaf rust caused by Puccinia recondita f. sp. tritici is one of the most destructive and widely distributed diseases of wheat. The most effective and economical method to control leaf rust is through breeding resistant cultivars (Caldwell, 1968). Slow rusting is a form of resistance where a susceptible host reaction is observed but the rate of disease development is slower when compared to susceptible cultivars. It has been reported that slow rusting resistance of wheat confers a more durable type of resistance (Kuhn, et al. 1978; Rajaram et al. 1984). Such resistance is the product of an interaction of the host and pathogen at different stages of pathogenesis (Kulkarni and Chopra, 1978). Cultivars may differ in their ability to retard disease development due to different combinations and degrees of expression of the various components that ultimately lead to the expression of slow rusting. The important components of slow rusting in leaf rust are: latent period, receptivity (number of uredia per unit area of leaf), uredium size, and spore production. There are reports on the inheritance and association of the components of slow rusting to leaf rust in wheat (Kuhn et al.1980, Lee and Shaner, 1985a; 1985b; Singh et al. 1990). However, these studies focused mainly on the inheritance of latent period and the association of the latent period with other components. The latent period has also been reported to be highly correlated with disease development in the field (Singh et al.1990; Shaner and Finney 1980).

To take advantage of more durable resistance, plant breeders require more information regarding the nature of inheritance and associations between the components of slow rusting. Furthermore, efficient selection for such resistance require methods for both greenhouse and field evaluations at seedling and early generation mature plant stages.

CIMMYT-derived wheat cultivars are grown on over 50.7 million hectares worldwide (Dalrymple, 1986). In a global context, durable disease resistance and genetic diversity are of paramount importance in CIMMYT's breeding program (Rajaram et al. 1988). Slow rusting resistance has been identified and utilized in CIMMYT's wheat breeding program. Singh et al. (1990) observed considerable variability for the components of slow rusting (partial resistance) in CIMMYT bread wheats. To use this variability efficiently in the breeding program, information on the nature of inheritance of the components are necessary.

The objectives of this study were to determine 1) the inheritance and associations of three components of slow leaf rusting in wheat and 2) the relationships of the components of slow rusting with slow disease development in the field using CIMMYT spring wheat genotypes.

MATERIALS AND METHODS

Greenhouse Study

Three components of slow rusting viz. latent period, receptivity, and uredium size were studied in the greenhouse at CIMMYT, El Batan, Mexico. The experimental materials consisted of two spring wheat parents, Sonoita 81 and Yecora 70 and 40 F6 progeny lines. Sonoita 81, is slow leaf rusting, in contrast to Yecora 70 (S. Rajaram, personal communication). The generations were advanced to F5 by single seed descent. Crosses were made in the field at the Centro de Investigaciones Agricolas del Noroeste (CIANO), Cd. Obregon, Mexico. F_1, F_2, and F_3 generations were grown in the greenhouse at the Oregon State University Campus, Corvallis, Oregon. F_4 and F_5 generations were grown in the field at CIANO, Cd. Obregon and CIMMYT, El Batan respectively. Seeds from a single F5 plant were bulked to form an F6 line. The susceptible cultivar 'Morocco' was included giving a total of 43 entries. Initially, sixty progeny lines were planted but only 40 of them with similar growth stages [(emergence of inflorescence completed; stage 58 - 59 on Zadoks scale), Zadoks et al., 1974] were selected for study. Parents were planted at two dates so that parents at a similar growth stage could be evaluated. Seeds from each experimental unit were planted in 2.54 liter plastic pots filled with a soil/compost mixture. Seeds were planted in 4 hills/pot (2 seeds/hill). Before inoculation four tillers with similar growth stage (one from each hill) were retained and the rest clipped-off.

Inoculation

Inoculation was done at the adult plant stage (stage 58 - 59 on Zadoks scale, Zadoks et al. 1974) with a single race of Puccinia recondita f.sp. tritici designated as MCD/SM [avirulence/virulence formula: Lr2a, 2b, 2c, 3ka, 9, 11, 16, 18, 19, 21, 23, 24, 25, 29, 30, 32, 33/Lr1, 3, 3bg, 10, 13, 14a, 14b, 15, 17, 20, 26, 27+31, 28; Long and Kolmer (1989), and R.P. Singh (personal communication)]. The adaxial surfaces of flag leaves were inoculated by uniform atomization of urediospores suspended in Soltrol 250 (a light-weight, nonphytotoxic mineral oil). The pressure of the atomizer was kept at 2.7 kg/cm. The suspension was prepared by adding 300 mg of urediospores to 200 ml of Soltrol.

Following inoculation, the plants were allowed to dry before they were put into a dark mist chamber for 18 hours. Three hours of light were then given without mist to allow the plants to dry before they were transferred to the greenhouse. The pots were placed in the greenhouse in a randomized complete block design on three benches. Each bench represented a replication. Greenhouse temperature was maintained at 18°C during nights and 22°C during days with a 12 hr day/night schedule.

Latent period was measured as the time from the day of inoculation to the day when 50% of the uredia had ruptured the epidermis. Flag leaves were checked daily starting from the third day after inoculation. Numbers of uredia rupturing the leaf epidermis each day were counted on each leaf until all the visible infection sites had ruptured. A uredium was considered ruptured when it

was visible without the assistance of magnification. The following formula was used to calculate latent period:

Latent period = $t_1 + (F/2 - t_1)(t_2 - t_1)/(nt_2 - nt_1)$

where F = final count of number of uredia, t_1 = day prior to 50% uredia rupture, t_2 = day after 50% uredia rupture, nt_1 = number of uredia ruptured on t_1, nt_2 = number of uredia ruptured on t_2.

To determine uredium size, the length and the width of five randomly-chosen uredia per leaf (20 uredia per experimental unit, except a few entries where there were less than five uredia on a leaf) were measured and uredia size was calculated according to the formula of Lee and Shaner (1985a) as follows:

Uredium size = length (mm) X width (mm) X $\pi/4$.

Uredia length and width were measured with a microcomparator (Finescale Inc. Orange, California) at the time when all uredia had matured.

Receptivity was determined as the number of uredia/cm^2 of leaf. The total number of uredia per leaf were counted and the leaf area was measured with a leaf area meter (LICOR Corp., Lincoln, NE) to calculate the number of uredia/cm^2.

Statistical and Genetic Analysis

Analyses of variance were conducted to determine differences for the components of slow rusting among the F6 lines. Narrow-sense heritability estimates were obtained using the following formula:

$h^2_n = \sigma^2_g/\sigma^2_p$;

σ^2_g and σ^2_p were estimated from the ANOVA table as follows:

$\sigma^2_g = (\sigma^2_L - \sigma^2_E)/r$, and $\sigma^2_p = \sigma^2_g + \sigma^2_E$

where h^2_n = heritability estimate in the narrow sense; σ^2_g = genetic variance; σ^2_L = variance of the F_6 lines, σ^2_E = error variance; and r = number of replications.

The number of genes controlling each component was estimated by Wright's (1968) method with some modification for the level of inbreeding of the progenies (F_6) as follows:

$$n = (GR)^2/4.27(\sigma^2_g F_6),$$

where GR = genotypic range, estimated as the difference between the mean response of two parents; $\sigma^2_g F_6$ = genotypic variance of F_6 generation; and n = the estimated number of segregating genes.

The number of genes controlling the components of slow rusting was also measured using the method described by East (1916). In this method the F_6 lines were grouped into three classes: lines homozygous like the slow rusting parent (class I), lines homozygous like the susceptible parent (class II), and lines different than the parents (classIII). A line was considered similar to one of the parents on the basis of two criteria: (i) the mean (average of the three replications) of the line should not deviate from the mean of the respective parent on the basis of an LSD (5% level) test, and (ii) a line having a mean similar to the slow rusting parent should not be more susceptible than the slow rusting parent in any replication; on the other hand, a line having a mean similar to the susceptible parent should not have any value beyond the range of the susceptible parent toward resistance. The number of lines in these groups were tested against the expected ratio using a Chi-square test.

Associations among the components were studied by computing genetic and phenotypic correlation coefficients among all possible pairs of variables. The genetic (r_g) and phenotypic (r_p) correlations were calculated from the analysis of covariance as follows:

$$r_g = \sigma^2_{g1g2} / \sqrt{\sigma^2_{g1} \times \sigma^2_{g2}}$$

$$r_p = \sigma^2_{p1p2} / \sqrt{\sigma^2_{p1} \times \sigma^2_{p2}}$$

where, σ^2_{g1g2}, σ^2_{p1p2} are genetic and phenotypic covariances of a pair of components; σ^2_{g1} and σ^2_{g2} are genetic variances of the two components; σ^2_{p1} and σ^2_{p2} are phenotypic variances of the two components.

Field Study

Thirty-five entries common to those studied in the greenhouse were grown in the field with entries from other crosses. The experiment was planted at the Centro de Investigaciones Agricolas del Noroeste (CIANO) experiment station at Cd. Obregon, Mexico on 22 November, 1988 in a randomized complete block design with three replications. Each entry was hand-planted in a 1.5-m long single row plot. Seeds were spaced about 5 cm apart in the plots. One row of CIANO 79, a spring wheat cultivar which is highly resistant to the prevalent leaf rust races in the area, was planted between adjacent plots to reduce movement of spores among entries, and thus interplot interference.

The experimental plots were inoculated with the same race of leaf rust as was used in the greenhouse studies. Inoculum was suspended by mixing 250 mg of urediospores per liter of purified water, and two drops of surfactant (Tween 20) was added to this suspension. Inoculation was done when the

plants were at growth stage 28-29 of the Zadoks scale (Zadoks et al. 1974). Four tillers from both ends of each experimental plot were inoculated with the spore suspension using hypodermic needles by injecting into the boot. Uredia were observed on the terminal leaves from the inoculated tillers at 10-13 days after inoculation. However, heavy disease was not observed by 6 weeks post inoculation. Therefore, to ensure an epidemic, the plots were inoculated in the evenings of March 8, 9, 14, and 15 by spraying a spore suspension made from fresh inoculum collected from spreader rows used in the CIMMYT bread wheat nursery. The suspension was prepared by mixing urediospores at the rate of 0.025 mg/ml of water and adding two drops of Tween 20 per 5 liters of water. Inoculum was applied with a motorized backpack sprayer equipped with a 5 m boom carrying nozzles every 75 cm. The boom was held by two persons walking along the sides of the plots at a constant speed. Analysis of races from bulk collections from the experiment showed that the race MCD/SM was the predominant race (R.P. Singh, personal communication).

To measure the area under the leaf rust progress curve (AULRPC) three rust severity readings (based on modified Cobb scale, Peterson, et al. 1948) were recorded at weekly intervals. The first reading was taken 11 days after the last spray inoculation. Disease severity values of the third reading were considered the final rust severity (FRS). Details of the field study is described in chapter I.

The relationship of each component (studied in the greenhouse) with the disease development in the field was studied by calculating the correlation coefficient of each component with AULRPC and FRS.

RESULTS AND DISCUSSION

Differences among the progeny for all three components of slow rusting were observed. Seedling and adult plant reactions [on a 0 to 4 scale (Roelfs, 1985)] were recorded for the two parents and the susceptible check Morocco. Morocco and Yecora 70 had a reaction type '4' in both seedling and adult plant stages, whereas Sonoita 81, the slow rusting parent, had a reaction type '3' in both stages of growth. No hypersensitive or low reaction type resistance was observed in these host genotypes against this particular leaf rust race. Only adult plant reaction types were recorded for the progeny. All progeny had a high reaction type ('3$^-$' to '4'). Mean responses of the parents and F_6 progeny, and the range of the F_6 progeny for different components are given in Table 2.1. The means for latent period and uredium size for Morocco are also provided. No data were obtained for receptivity of Morocco.

Inheritance of the components of slow rusting

Latent Period

Sonoita 81, the slow rusting parent, had a latent period 3.11 days longer than Yecora 70. The latent period for Yecora 70 was almost one day (0.93) longer than Morocco (Table 2.1). Thus Sonoita 81 had a 39% and 57% increased length of latent period when expressed as percentage of the susceptible genotypes Yecora 70 and Morocco, respectively. The distribution of F_6 family mean latent period was continuous between slow rusting and fast rusting parents (Fig.2.1). However, continuous distribution of progenies for a

trait do not necessarily mean that the trait is polygenic (Kuhn, et al. 1980; Lee and Shaner 1985a; Bjarko and Line 1988). Continuous distribution of the progeny lines might result from low heritability or segregation of many genes, or both (Allard, 1960).

Progeny with a 0.88 day longer latent period than the slow rusting parent Sonoita 81 was observed. Progeny genotype with a 0.46 day shorter latent period than Yecora 70 was identified, but this latent period was not as short as Morocco (Table 2.1). The mean latent period of the F6 progenies (9.33) was close to the midparental value (9.61) suggesting that nature of inheritance for this trait is controlled by genes functioning in an additive manner.

The narrow-sense heritability estimate for latent period was 57.2%. The estimate of the number of genes controlling an extended latent period in Sonoita 81 was two or three (Table 2.3 and 2.4). This number of genes is similar to that reported by Kuhn et al. (1980) and Lee and Shaner (1985a) who identified two genes for longer latent period in slow leaf rusting wheat genotypes.

Receptivity

Sonoita 81 had a 81% reduced receptivity when expressed as percentage of the susceptible parent Yecora 70. The mean number of uredia/cm^2 for the F_6 progeny was 1.55, which is higher than the mean for Sonoita 81 but lower than that for Yecora 70. Reduced receptivity of slow rusting wheat genotypes has been reported by others (Milus and Line, 1980; Rajaram et al. 1988; Singh et al. 1990). The distribution of F_6 family mean receptivity was discrete (Fig. 2.2) which indicates that the trait is not controlled by polygenes. Progeny with the lowest

and highest receptivity had values of 0.47 and 5.03, respectively. Transgressive segregation [based on a $LSD_{(.05)}$] toward greater receptivity was observed.

Narrow-sense heritability was 47.1%, which was the lowest of all components studied. Low heritability of receptivity might result from less uniform inoculation of the leaves of the experimental materials. This might also occur from a greater influence of environmental variation on this component. Parlevliet and Kuiper (1977) and Parlevliet (1986) working with leaf rust (Puccinia hordei) of barley also reported larger environmental influences for receptivity. The heritability estimate for receptivity in our study was still high enough to allow genetic gain for this component through selection. The estimate of the number of genes segregating for receptivity was three or four (Tables 2.3 and 2.4).

Uredium size

Sonoita 81, Yecora 70, and the susceptible check Morocco had mean uredium sizes of 0.057, 0.147, and 0.252, respectively. The slow rusting parent Sonoita 81 had 61% and 77% reduced uredium size when compared to the susceptible parent Yecora 70 and check Morocco, respectively. Reduced uredia size associated with slow rusting wheat cultivars has been reported by other authors (Ohm and Shaner, 1976; Shaner, et al. 1978; Rajaram et al. 1988; Singh et al. 1990). The distribution of F_6 family mean uredia size was continuous between the slow rusting and fast rusting parents (Fig. 2.3). However, the differences from the parental values were not high as for other components (0.005 below the slow rusting parent and 0.008 above the susceptible parent). Mean uredium size (0.102) of the F6 progenies was equal to the midparental

value. The narrow-sense heritability estimate (62.5%) for uredium size was the highest of all components studied. This moderately high heritability estimate indicates that selection would be effective to reduce uredium size. The estimate of the number of genes involved suggests that three or four genes reduced uredium size in the slow rusting cultivar Sonoita 81 (Tables 2.3 and 2.4).

Selection Effectiveness

Based on the reasonably high narrow-sense heritability estimates and oligogenic nature of the inheritance it would appear that selection for any of the three components of slow rusting would be effective in early segregating generations of this cross. The larger environmental variance associated with receptivity would suggest that phenotypic selection for the other two components might be more effective.

Associations Among the Components of Slow Rusting

Genotypic and phenotypic correlation coefficients are presented in Table 2.5. Phenotypic correlation reflects the observed relationship between traits resulting from combined effects of genotype and environment, while genotypic correlation estimates the association between traits resulting from pleiotropy or linkage (Pandey and Gritton, 1975; Nienhuis and Singh, 1986). Pandey and Gritton (1975) noted that no suitable test of significance for genotypic correlations is available. Therefore, their primary use is to strengthen interpretations based on phenotypic correlations, and in better predicting correlated responses to selection (Nienhuis and Singh, 1986).

Both genetic and phenotypic correlations had the same sign but differed in magnitude, with genetic correlations always being higher. A large negative relationship between latent period and uredium size (r_g = -0.809 and r_p = -0.618) was seen. Moderately high negative correlation were also observed between latent period and receptivity (Table 2.5). The correlations between uredium size and receptivity were positive and significant but had lower values than the other associations (Table 2.5). Associations observed in this study are in agreement with other reports regarding the components of slow rusting to leaf rust in wheat (Kuhn et al. 1980, Lee and Shaner, 1985b; Singh et al. 1990). Singh et al. (1990) working with spring wheat cultivars/lines observed moderately high negative correlations of latent period with uredium size and receptivity. Lee and Shaner (1985a) and Kuhn et al.(1980) found moderately high negative correlation between latent period and uredium size. Parlevliet (1986) observed a similar result in two barley crosses infected with leaf rust. Strong correlation and the ability to describe the association of latent period and receptivity in one population of F_3 lines over the two crosses by one regression equation led him to suggest a pleiotropic association between these two components.

The correlations between receptivity and latent period was not high enough to conclude pleiotropic gene action in the present study. However, the possibility of a pleiotropic association among the components could not be overlooked, as the correlation value between latent period and uredium size was high. The lower correlation value (Table 2.5) between latent period and

receptivity might result from the fact that receptivity was more prone to environmental variation.

Phenotypic correlation between the components of slow rusting and disease development in the field

Area under the leaf rust progress curve (AULRPC) obtained from the field disease data showed a significant positive correlation (r = 0.64) with uredium size and negative correlation with latent period (r = -0.55) (Table 2.6). The correlation between AULRPC and receptivity was not significant (r = 0.26).

Final rust severity (FRS) was also positively correlated with uredium size (r = 0.68) and negatively correlated with latent period (r = -0.59). The correlation between receptivity and FRS was positive but nonsignificant (r = 0.24) (Table 2.6). The correlation coefficient between AULRPC and FRS was high (0.98). That AULRPC is negatively correlated with latent period and uredium size and positively correlated with receptivity and uredium size has also been previously reported (Shaner and Finney, 1980; Singh et al. 1990). Our results, supported by other evidence, suggest that effective selection for slow rusting genotypes can be practiced in the field based on AULRPC and in the greenhouse based on resistance components, preferably latent period and uredium size. In addition our data suggest that selection for slow rusting genotypes can also be based on FRS in the field. Thus, if resources are limited and three or more readings are not available to compute AULRPC, FRS data would still help selecting slow rusting genotypes.

The moderately high correlations of latent period and uredium size with slow rust development in the field does not suggest a pleiotropic association between slow rusting and its components. However, the estimates of the number of genes controlling slow rusting in the field and the components of slow rusting in this particular cross was similar, which indicates the possibility that the genes for slow rusting pleiotropically controls various components of slow rusting. A similar gene action for slow rusting resistance (partial resistance) to leaf rust in barley has been suggested by Parlevliet (1986).

In conclusion, strong associations exist among various components of slow leaf rusting in these wheat genotypes. Results do not exclude the possibility of close linkage or pleiotropic association among the components as reported for leaf rust in barley by Parlevliet (1986). Estimates of the number of genes for latent period, uredium size, and receptivity obtained under greenhouse conditions were between three and four. The narrow-sense heritability estimates were reasonably high. Slow rusting genotypes can be selected in the early segregating populations from crosses between slow and fast rusting genotypes on the basis of resistance components preferably latent period or uredium size in the greenhouse evaluation and on the basis of AULRPC or FRS in the field evaluation.

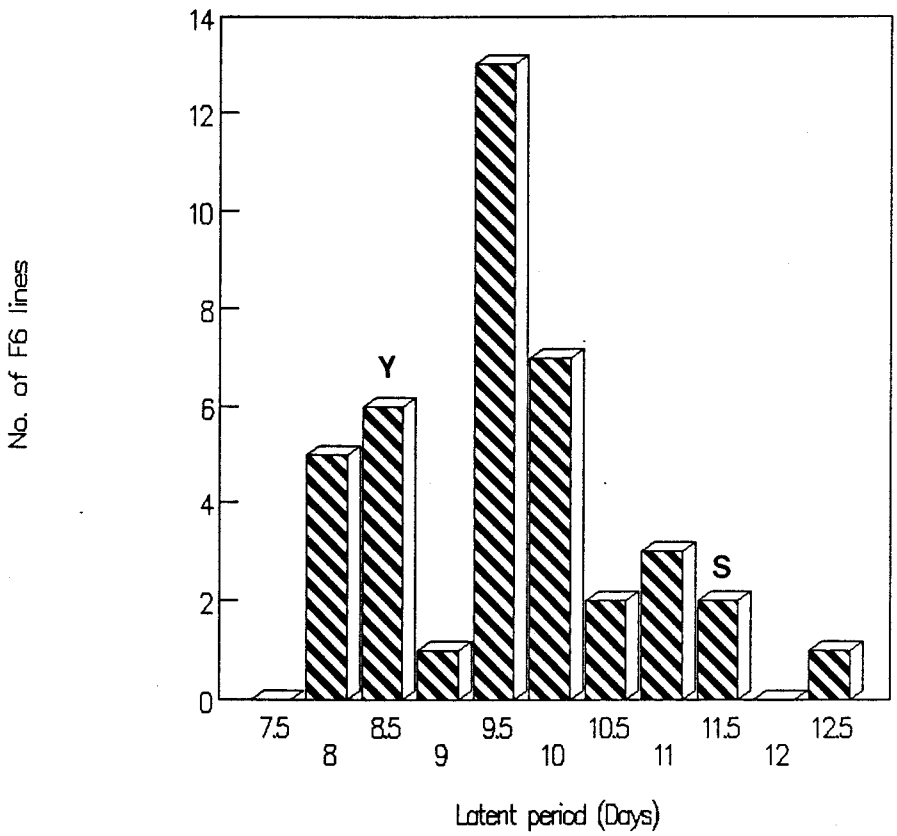

Fig.2.1. Frequency distribution for latent period of F_6 lines of a spring wheat cross infected with leaf rust race MCD/SM in the greenhouse. (Parents Y = Yecora 70, S = Sonoita 81) are indicated above the class in which they fall.

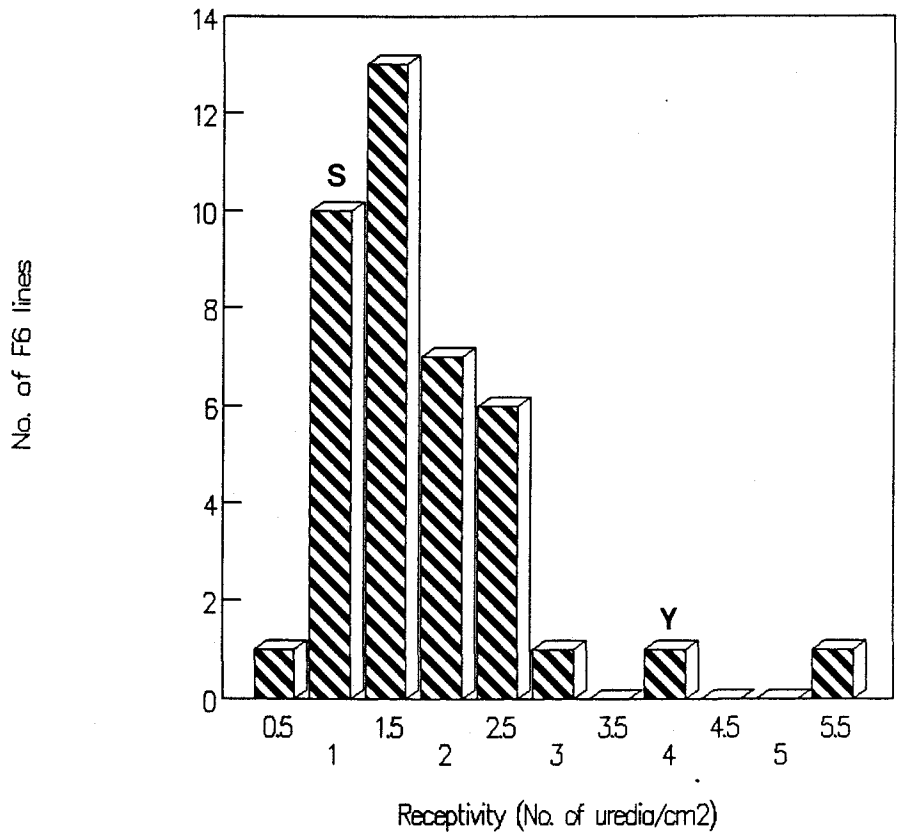

Fig.2.2. Frequency distribution for receptivity of F_6 lines of a spring wheat cross infected with leaf rust race MCD/SM in the greenhouse. Parents (Y = Yecora 70, S = Sonoita 81) are indicated above the class in which they fall.

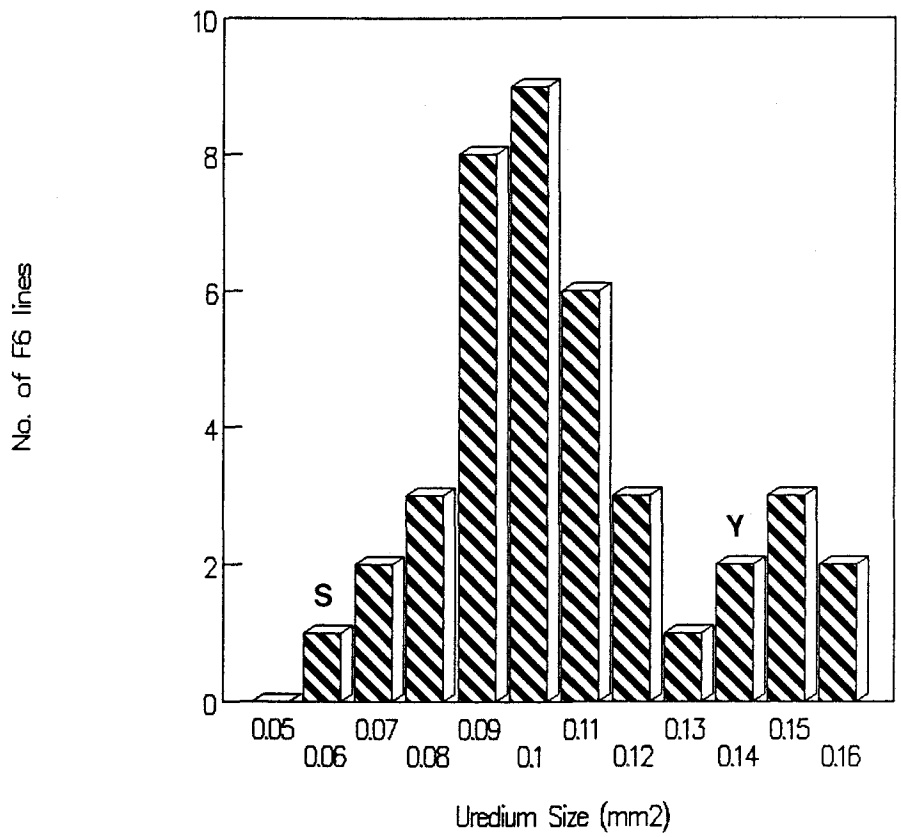

Fig. 2.3. Frequency distribution for uredium size of F_6 lines of a spring wheat cross infected with leaf rust race MCD/SM in the greenhouse. Parents (Y = Yecora 70, S = Sonoita 81) are indicated above the class in which they fall.

Table 2.1. Mean and standard error (S.E.) for the slow rusting parent Sonoita 81, susceptible parent Yecora 70, susceptible check Morocco*, and F_6 progenies and range for F_6 progenies for latent period, receptivity, and uredium size infected with Puccinia recondita f.sp. tritici in the greenhouse

		Latent period (Days)	Receptivity (No. of uredia/cm^2)	Uredium size (mm^2)
Sonoita 81	Mean	11.16	0.70	0.057
	S.E.(±)	0.05	0.15	0.004
Yecora 70	Mean	8.05	3.66	0.147
	S.E.(±)	0.27	0.83	0.010
Morocco	Mean	7.13	-	0.252
	S.E.(±)	0.18	-	0.014
F_6 lines	Mean	9.33	1.55	0.102
	S.E.(±)	0.16	0.14	0.004
	Range	7.59 - 12.0	0.47 - 5.03	0.052 - 0.155

*, Data on receptivity for Morocco were not recorded.

Table 2.2. Estimates of genotypic, error, and phenotypic variances and heritability (narrow-sense) for latent period, receptivity, and uredium size in F6 generation of the cross between the slow leaf rusting wheat cultivar Sonoita 81 and fast rusting cultivar Yecora 70 infected with Puccinia recondita f. sp. tritici in the greenhouse.

Components	Parameters			
	Genotypic variance	Error variance	Phenotypic variance	Heritability estimates (%) (narrow-sense)
Latent period	0.847	0.634	1.481	57.2
Receptivity	0.545	0.613	1.158	47.1
Uredium size	0.0005	0.0003	0.0008	62.5

Table 2.3. Number of F_6 lines having genotypes like the slow rusting parent (Class I), the susceptible parent (Class II), and those that are different than the parents (Class III) for three components of slow rusting evaluated in the greenhouse

	Number of F6 lines			
Components	Total	Class I	Class II	Class III
Latent period	40	2	4	34
Receptivity	40	6	3	31
Uredium size	40	2	4	34

Table 2.4. Estimates of number of segregating genes for latent period, receptivity, and uredium size in the cross Sonoita 81 X Yecora 70 infected with Puccinia recondita f.sp. tritici in the greenhouse

Components	Methods	Number of genes	Probability
Latent period	Wright's (1968)	2.7	
	East's (1916)	3.0	0.20 - 0.50
Receptivity	Wright's (1968)	3.8	
	East's (1916)	3.0	0.20 - 0.50
Uredium size	Wright's (1968)	3.9	
	East's (1916)	3.0	0.20 - 0.50

Table 2.5. Genetic (r_g) and phenotypic (r_p) correlations among latent period, receptivity, and uredium size in the F6 generation of the cross, Sonoita 81 X Yecora 70 infected with P. recondita f.sp. tritici in the greenhouse

		Receptivity		Uredium size
Latent period	r_g	-0.50		-0.81
	r_p	-0.41**		-0.62**
Receptivity			r_g	0.28
			r_p	0.26*

** and *, significant at $P<0.01$ and $P<0.05$, respectively.

Table 2.6. Correlation of area under the leaf rust progress curve (AULRPC) and final rust severity (FRS) from the field with latent period, receptivity, and uredium size obtained from the greenhouse in the F6 generation of the cross between Sonoita 81 and Yecora 70 infected with P. recondita f.sp. tritici

	Latent period	Receptivity	Uredium size	FRS
AULRPC	-0.55**	0.26	0.64**	0.98**
FRS	-0.59**	0.24	0.68**	

**, significant at $P<0.01$.

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CONCLUSIONS

Two experiments were conducted to study the nature of inheritance and associations of slow rusting and three components of slow rusting resistance to leaf rust in wheat. The following conclusions were drawn:

1. Slow rusting resistance as measured by area under the leaf rust progress curve was controlled by two to four genes, depending on the parents used in the cross. Moderately high to high narrow-sense heritabilty estimates were calculated for most crosses. Gene action was predominantly additive, but additive X additive epistasis was also important. Early generation selection for slow leaf rusting in wheat should be effective.

2. Associations between slow rusting and plant maturity were low and negative and there was no relationship between slow rusting and plant height. In general, selection for slow rusting, would not be influenced by either plant maturity or plant height.

3. Strong and favorable associations exist among various components of slow leaf rusting. Selection for one component will indirectly select for the others, in the desired direction.

4. Estimates of number of genes for latent period, uredium size, and receptivity were between three and four. Narrow-sense heritability estimates for the components were reasonably high. Selection for these components should be effective in early generation segregating populations.

5. Latent period and uredium size had reasonably high correlations with both AULRPC and FRS. Slow rusting genotypes can be selected on the basis of

AULRPC or FRS in the field and on the basis of resistance components, preferably latent period and uredium size, in the greenhouse.

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APPENDIX

Appendix Table 1. Pedigree of parental cultivars/lines used in the diallel cross

Cultivars/ lines	Cross	Cross No.& Selection
Yecora 70	Bluebird # 2	II23584-26Y-2M-1Y-0M
Sonoita 81	TRM//KAL/BB	CM37130-15Y-1M-3Y-0M
Tanager'S'	Sis'S'/PVN'S'	CM30697-10M-1Y-10M-1Y-1B-0Y
Galvez 87	BB/GLL/CARP/3/PVN'S'	CM33483-C-7M-1Y-0M-5B-0Y
Ures 81	Veery # 2	CM33027-F-12M-1Y-4M--2Y-2M-0Y
Moncho'S'	WE/GTO//KAL/BB	CM8288-A-3M-6Y-5M-1Y-0M

Source: Villareal and Rajaram (1988 revised)

Appendix Table 2. Summary of climatic data on a per month basis for CIANO Field Laboratory, growing season 1988-89

Month	Precipitation (mm)	Relative humidity	Temperature °C	
			Average Max.	Average Min.
November	0.00	66.20	29.79	11.51
December	30.30	74.61	24.26	8.25
January	18.50	77.55	22.16	6.14
February	62.10	78.25	24.79	9.57
March	0.00	81.39	27.62	10.36
April	0.00	-	33.04	13.40