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Title: Inheritance of Resistance to Septoria Leaf Blotch in Selected Spring Wheat Genotypes (*Triticum aestivum L.*)

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Septoria leaf blotch of wheat is a major biotic factor limiting the grain yield. To determine the nature of inheritance involving selected genotypes, three resistant semidwarf spring wheat lines exhibiting durable global resistance and one susceptible cultivar were crossed in all possible combinations, excluding reciprocals. Parents, F1, F2, and F3 generations were inoculated with one pathogenic strain of Septoria tritici and evaluated under field conditions. Data were collected on an individual plant basis. F2 and F3 frequency distributions were computed to determine the nature of inheritance. Combining ability analysis of the 4x4 diallel cross and narrow-sense heritability were employed to estimate the nature of gene action. Phenotypic correlations were obtained to examined the possible association between disease severity traits and their relationship with heading date and plant height.

The continuous distribution of the F2 and F3 populations among crosses made it impossible to classify plants into discrete classes in crosses between resistant x susceptible genotypes. Mean values of the disease traits Septoria progress coefficient, Relative coefficient of infection, and Septoria severity of flag leaf among the

segregating populations were similar to the midparent values. Transgressive segregation was also observed in the F2 and F3 suggesting that parents had different resistance genes. Additive gene effects were found to be the major component of variation although nonadditive gene action played an important role in the expression of all three disease traits. The resistant parents Bobwhite"S" and Kavkaz/K4500 L.A.4 were found to have the largest negative general combining ability effects for the disease traits suggesting that these parents would be the best source for resistance to Septoria leaf blotch. High general combining ability and high narrow sense heritability estimates in the F3 population, indicated that substantial progress for resistance to Septoria tritici would be effective selecting in this generation. Of the three disease measures it would appear that selection for the lowest percentage of Septoria infection on the flag leaf would provide the most progress in developing resistant cultivars. Moderate and low negative phenotypic correlations were found among generations for the disease traits with heading date and plant height. From the results of this study the selection of early maturing short stature progeny would be possible within the genetic materials employed in this study.

INHERITANCE OF RESISTANCE TO SEPTORIA LEAF BLOTCH IN SELECTED SPRING BREAD WHEAT GENOTYPES (Triticum aestivum L.)

by

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IN DEDICATION TO:

MY FAMILY

Expression of love in my life.

THE WHEAT PROGRAM AT CIMMYT

For being so closely involved in my professional formation.
I couldn't be in better hands.

And last, but definitely not least, **ALL MY FRIENDS** and anyone else who has given me care and time, more important to me than ever before.

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TABLE OF CONTENTS

LIST OF FIGURES

FIGURE PAGE

LIST OF TABLES

TABLE PAGE

LIST OF APPENDIX TABLES

TABLE		PAGE

TABLE PAGE

INHERITANCE OF RESISTANCE TO SEPTORIA LEAF BLOTCH IN SELECTED SPRING BREAD WHEAT GENOTYPES (Triticum aestivum L.)

INTRODUCTION

Septoria leaf blotch of wheat, a disease caused by Septoria tritici Rob ex Desm. (perfect state: Mycosphaerella graminicola [Fuckel] Schroeter), is considered one of the major diseases in high rainfall wheat growing areas of the world (Saari and Wilcoxson 1974, Mann et al. 1985, Eyal et al. 1985, Beuningen and Kholi 1988). Prior to 1970, most of the semidwarf cultivars were highly susceptible to Septoria leaf blotch. This was particularly true in North Africa and Middle East which experienced the epidemic of the disease in 1968.

Breeding for resistance to this disease is being undertaken at many institutions around the world as resistant cultivars represent the most economic and practical method of control (Rajaram and Dubin 1977). Simply inherited resistance genes have been identified and transferred to susceptible wheat cultivars. However, wheat cultivars reported to be resistant in one environment have not proven resistant in other locations (Eyal et al. 1985). This suggested that more a durable type of resistance to Septoria tritici is required.

Differences in degree of symptom expression and yield reductions have been observed in the presence of the pathogen; however, knowledge of the genetic basis of resistance is limited. These difficulties, together with possible pathotype specialization in S. tritici has complicated the genetic transfer of the resistance into otherwise acceptable genotypes (Eyal et al. 1973, Danon et al. 1982).

Sources of resistance to S. tritici have been identified and reported (Narvaez and Caldwell 1957, Shaner et al. 1975, Danon et al. 1982, Rajaram et al. 1984, Eyal et al. 1985). In spring wheat, sources of resistance were derived from Russian winter wheats Aurora, Kavkaz and Bezostaya 1 and from South American wheat Frontana and its derivates (Rajaram et al. 1984).

Associations between desired trait and other traits have been observed (Shaner et al. 1975, Rosielle and Brown 1979, Brokenshire 1980, Eyal 1981, Danon et al 1982, and Baltazar 1987). These associations have been particularly apparent with enhanced disease expression in short and early maturity genotypes (Lee and Gough 1984, Baltazar 1987, Beuningen and Kholi 1988, and Rajaram 1989). In addition, a National Academic of Science publication (1970) infers possible linkage between semidwarf characteristics of bread wheat and general vulnerability to Septoria leaf blotch. Therefore, to be successful breeding efforts must concentrate on the components of resistance that are independent of these phenotypic traits and incorporate resistance to S. tritici into agronomically acceptable wheat cultivars.

The objectives of this study were 1) To determine the mode of inheritance of resistance to Septoria tritici in selected germplasm expressing more durable levels of resistance in spring wheat growing areas, and 2) To examine the relationships between plant height, heading date and severity of Septoria leaf blotch infection.

LITERATURE REVIEW

A. Importance and Distribution of Septoria tritici

Septoria leaf blotch is a major biotic constraint to wheat production in many parts of the world. Geographic distribution and economic importance of this disease have been reviewed (Shipton et al. 1971, Saari and Wilcoxson 1974, Caldwell 1976, Royle et al. 1986, Eyal et al. 1987, and Beuningen and Kholi 1988). Septoria tritici is widespread, being found in several regions of the United States, Central and South America, Southern Australia, New Zealand, Mediterranean Coastal regions, East Africa, South Africa, and a number of European countries (Eyal et al. 1987). During the past 25 years Septoria leaf blotch has increased and has become a major limiting factor to wheat production.

According to Shaner (1981), the asexual stage of Septoria leaf blotch of wheat, Septoria tritici, has been known since 1894; however, the sexual stage of the casual agent Mycosphaerella graminicola, was not recognized until 1972. Septoria tritici belongs to the Class Fungi Imperfecti and is classified in the Sphaeropsidales Order. Its sexual stage belongs to the Class Ascomycetes, Subclass Loculoascomycetes, Order Dothideales, and Family Dothideaceae (Schaner and Sanderson, 1985, and Eyal et al. 1987).

A resolution of the Second International Septoria Workshop opted that the taxonomic name of the fungi should be based on the sexual stage, and the common name of the disease on the asexual stage (Eyal et al. 1987). Therefore, Septoria tritici blotch is the preferred name of the disease and Mycosphaerella graminicola the causal agent. The sexual stage has been reported in several countries; however, it is the asexual stage of the fungus that is the most destructive on wheat.

Rajaram and Dubin (1977) observed that Septoria leaf blotch was reported 40 years ago in Tunisia and the Mediterranean Coastal regions, causing serious yield reduction. Rajaram (1989) noted that in the early 1970's, semidwarf cultivars were especially susceptible to S. tritici in the Mediterranean regions. It has been inferred by several researchers that the main reason for this change in the 1970's was due to the replacement of tall, late maturing, traditional cultivars with higher yielding semidwarf cultivars which are more susceptible. In a review of the plant diseases in Asia and Africa, Saari and Wilcoxson (1974) noted that the continuous replacement of local tall wheats by semidwarfs, in high rainfall conditions, and the modifications in agronomic practices contributed to the occurrence of severe epiphytotics of S. tritici. However, they also observed that severe infection had been observed in traditional cultivars when grown under high soil fertility conditions. These authors concluded that the semidwarf stature was not responsible for the increased incidence of the Septoria in wheat, but the disease was severe on the new semidwarf cultivars than the traditional tall cultivars because the former were selected in the absence of this pathogen.

Severity of the disease is closely related to rainfall frequency and cool weather (Shaner and Finney 1976, Shaner 1981, and Hess and Shaner 1987). According to Shaner (1981), and Eyal et al. (1987) prolonged periods of moisture is important in all stages of disease development: from inoculum production through liberation, dispersal, penetration, lesion development and subsequent pycnidial development.

Eyal (1981) reported that S. tritici affects leaves and sheaths and under severe epidemics, shrivelling of leaves and defoliation may result in shrivelled grains in some cultivars with plant death under extreme conditions. In addition, the vertical progress of the disease from the base to the top of the plant is strongly affected by plant stature (Eyal et al. 1983). Similar results were obtained by Re (1988) who observed a faster progress of S. tritici in dwarf than in a semidwarf winter statured genotypes.

B. Phenotypic Traits Association

In the course of natural and artificial selection, traits have evolved to limit the damage caused by micro-organisms. Plant characteristics like canopy structure, plant height, and late maturity, have contributed to the apparent resistance to S. tritici (Eyal and Ziv 1974, Shaner et al. 1975, Brokenshire 1980, and Eyal et al. 1983).

The development of semidwarf cultivars, resulting in a more dense canopy structure, may have resulted in a microclimate that is more favorable to the development of S. tritici. According to Eyal and Ziv (1974), the compactness of the internodes in semidwarf cultivars increases the possibility for S. tritici to reach the upper plant parts easily even under moderate disease conditions. Brokenshire

(1980), suggested that semidwarf cultivars may produce an ideal microclimate within the crop canopy for S. tritici development. Traditional tall cultivars with lower above surface biomass resulted in less favorable microclimates for disease development. Therefore, the chances of disease dissemination to upper portions of semidwarf wheat plants is greater when the distance to be traveled by the pycniospores is less. Bahat et al. 1980, corroborated this association and observed that the vertical progress of S. tritici from the base to the top of the plant is affected by the distance between consecutive leaves.

Early maturing semidwarf wheat genotypes are generally more susceptible to S. tritici. Rosielle (1972), Danon et al. (1982), Eyal et al. (1983), and Beuningen and Kohli (1988), confirmed this association and observed that a considerable number of late maturing wheat cultivars tended to show ample distribution of resistance to S. tritici under natural and artificial inoculation in the field. However, Shaner et al. (1975), and Beuningen and Kohli (1988), observed that this kind of resistance might be an escape mechanism, as periods of greatest disease development occurs between flowering and maturity. Therefore, genotypes that pass through these stages earlier are exposed to an increased frequency of rain and cool weather, favorable conditions for disease development.

Selection for resistance to S. tritici has generally produced tall, and late maturity cultivars. According to Mann et al. (1985) and Rajaram (1989), considerable genetic variation in height and maturity exists in the spring wheat germplasm selected at the International Maize and Wheat Improvement Center

(CIMMYT). However, breeding has been complicated as Septoria leaf blotch resistance tend to be associated with tall and late maturity plant types, two characteristics considered undesirable in many wheat production regions where Septoria leaf blotch is a potential problem.

Studies concerning these traits and disease expression show a clear tendency to be associated with the possibility of genetic linkages being involved. Shaner et al. (1975) suggested that genes for resistance are associated with late maturity genotypes through linkage, or are more strongly expressed in a late maturity genotypes. Rosielle and Brown (1979), reported resistance to S. tritici scores to be negatively associated with heading date and plant height, but these correlations were not a major obstacle in the selection of early, resistant, semidwarf wheats in Australia.

A study to determine the relationship between plant stature, maturity and susceptibility was concluded by Danon et al. (1982). They found small negative correlations between plant height and pycnidial coverage of S. tritici suggesting that neither strong linkage nor pleiotropy were involved. These authors also obtained moderate negative correlation between heading date and resistance to S. tritici. They concluded that this latter association may be due to genetic linkage.

Based on an analysis of progeny of isogenetic lines of winter wheat containing dwarfing genes Rht1 and Rht2, Baltazar (1987) reported high negative correlations between S. tritici severity and short stature in F2 populations; however the presence of short resistant and tall susceptible progeny supported the hypothesis that linkage rather than pleiotropism determined the association between plant height and Septoria severity.

Using F1, F2, F3, and backcross segregating populations from a cross between two winter wheat lines, Camacho-Casas (1989) conducted a genetic study of the possible association between heading date, plant height and resistance to S. tritici. He reported negative association of heading date and plant height with S. tritici severity. He noted that although these results confirmed previous reports regarding these association, it was evident in this study that all of the variation observed for disease severity could not be explained by the variation in either heading date or plant height. Suggesting that genetic resistance per se was independent from heading date and plant height.

C. Inheritance of Resistance

The wide spread introduction of semidwarf wheats in the 1960's was successful as such cultivars were widely adapted, had high yield potential, and were resistant to the most predominant diseases. Nevertheless, in some high rainfall areas with periods of wet weather and cool temperatures which favor the development of S. tritici, semidwarf wheats were susceptible to this fungus than the local land races varieties (Saari and Wilcoxson, 1974). Thus, when S. tritici proved to be an important yield limitation, an effort to identify and incorporate sources of resistance by breeders and pathologists was made (Shipton et al. 1971, Rajaram and Dubin 1977, Eyal et al 1985, and Beuningen and Kholi 1988).

Modes of inheritance of resistance and gene action have been reported to be largely qualitative. Narvaez and Caldwell (1957) studied the resistance of winter wheat to S. tritici using F1, F2, F3, and backcross progenies derived from crosses among the cultivars 'Nabob'(resistant), and 'Knox', and 'Vermillon'(susceptible). They found that the resistance of the cultivar 'Nabob' appeared to be controlled by two independent, partially dominant genes with additive effects. In an additional study these authors reported that resistance of the cultivars 'Lerma 52' and 'P14', was controlled by a single dominant gene.

A similar pattern of resistance was observed in studies of the F1, F2, and backcross progenies of 'Bulgaria 88' (Rillo and Caldwell, 1966). This resistance has been particularly effective in Indiana, and provided resistance in 'Oasis', a soft red winter wheat cultivar released for the region (Shaner et al. 1975). In a later study, Shaner and Buechley (1989) reported that the resistance in the cultivar 'Oasis' was controlled by a single partially dominant gene. The same report describes the resistance of the cultivars 'Sullivan' and 'Purdue 72626' to be controlled by a single dominant gene. These authors indicated that 'Sullivan' 'Oasis', and 'Purdue 72626' all carry the same single gene for resistance to S. tritici, derived from 'Bulgaria 88'.

Resistance to S. tritici in the spring cultivars 'IAS 20' and 'Veranopolis' appeared to be determined by a single gene (Rosielle and Brown, 1979). These authors observed that the inheritance patterns of resistance in these two cultivars were similar when they were crossed with the susceptible Australian spring cultivar

'Gamenya'. Since both have common ancestry, these authors concluded that 'IAS 20' and 'Veranopolis' may carry the same gene for resistance.

Resistance in 'Carifen 12' wheat cultivar from Chile was found to be due to a single dominant gene (Lee and Gough, 1984). A similar pattern of resistance was observed in the winter wheat cultivar 'Vilmorin' which also exhibited single gene inheritance (Gough and Smith, 1985).

By using several spring and winter wheat sources of resistance to S. tritici, Wilson (1985) reported a predominance of single dominant gene mode of inheritance for resistance to Septoria leaf blotch. However, other patterns of inheritance were also found by this author who described cases of duplicate dominant genes and single incomplete dominant gene.

According to Rosielle and Brown (1979) the inheritance of resistance in the spring wheat cultivar 'Seabreeze' is determined by three recessive genes. While Wilson (1985) reported inheritance of resistance to be controlled by two recessive genes in the same cultivar.

Using a gene for gene approach, Eyal et al. (1985) evaluated the virulence of 97 isolates of S. tritici collected from several spring and winter wheats in 22 countries. Using These isolates they determined two genes for resistance to Septoria leaf blotch in the winter wheats 'Aurora', 'Bezostaya 1', and 'Kavkaz', seven genes were estimated in the CIMMYT line Kavkaz/K4500 L.A.4, and four in Bobwhite "S". According to these authors, Bobwhite "S" and Kavkaz/K4500 L.A.4 expressed the highest level of resistance among six geographical Septoria regions. They also reported that virulence frequencies of isolates varied considerably among the Septoria regions with Mexico and Uruguay having the broadest virulence combinations.

Based on an analysis of F1 and F2 progeny, Danon et al. (1982) found one and two genes controlling the inheritance of resistant to S. tritici in the winter wheats 'Bezostaya 1' and 'Oasis' respectively. However, in earlier study (Shaner et al. 1975) found that the resistance in the cultivar Oasis was controlled by one gene. Danon et al. (1982) proposed that the inconsistency on whether Oasis had one or several genes controlling resistance may be due to the physiologic specialization of S. tritici.

In a later study, Danon and Eyal (1989) confirmed that the number of genes controlling resistance in the winter wheats 'Aurora', 'Bezostaya 1', 'Kavkaz' and 'Trakia' was small (usually two genes). These authors also found that the resistance in 'Colotana' and 'Klein Titan' derived from the cultivar 'Frontana' was controlled by a small number of genes, probably two which result in additive effects.

Using generation means analysis with seedlings, Van Ginkel and Sharen (1987a) studied crosses of thirteen related durum wheats resistant to S. tritici for both number of lesions and percent necrosis. Additive as well as dominant gene effects were suggested. Epistatic gene effects were rare.

Camacho-Casas (1989) observed that gene expression of resistance in the progeny of two winter wheats cultivars were attributed to both additive and nonadditive genetics effects. He concluded that dominance and epistasis were in a higher magnitude than additive genetic effects.

From the literature it appears that resistance to S. tritici is a qualitatively inherited trait. However, the number of genes and nature of the gene action varies depending on the genetic background of the cultivars selected. The question of whether some cultivars may confer a more durable type of resistance remains to be investigated and is the focus of this investigation

MATERIALS AND METHODS

Spring wheat lines consisting of three semidwarf resistant genotypes and one cultivar susceptible to Septoria tritici were selected from germplasm developed by the International Maize and Wheat Improvement Center (CIMMYT). The resistant lines included: Bobwhite"S" CM33203-K-9M-2Y-1M-1Y-1M-0Y, Kavkaz/K4500 L.A.4. SWM0176-3M-1Y-10Y-1Y-1M-0Y, and Oasis/Torim SWM7094-1Y-1Y-0YA-0J. Ciano 79 was used as the common susceptible parent. The three parents were found resistant to Septoria leaf blotch to global environments when tested in the International Septoria Screening Nursery (ISEPTON). These three resistant genotypes have demonstrated low levels of infection in high rainfall areas of Latin America, East Africa, Middle East, and North Africa.

All possible crosses were made excluding reciprocal at Toluca, Mexico in 1987. The F1's were grown at Cd. Obregon, Sonora, Mexico in 1987-88 and advanced to the F2 in the 1988 summer nursery at Toluca. During 1988-89 crop cycle 80 F2 plants from each of the six crosses were randomly chosen at Cd. Obregon to produce F3 populations.

Parents, F1, F2, and F3 populations from each cross combination were planted at CODAGEM[1], Toluca, Mexico. Parents, F1, and F2 populations were space planted. F1 plots were 2-rows, 1 meter long with 5 centimeters between

[1]Agriculture and Livestock Development Commission of Mexico State

plants, and 30 centimeters between rows. Parents and F2 were planted in 8-rows, 11 meters long, and 15 centimeters between plants, and 30 centimeters between rows.

The parents and randomly selected F3 lines were also space planted, using a split plot randomized block design with three replications. Crosses were used as main plots and F3 lines as subplots. Plots were 2-rows, 1 meter long with 5 centimeters between plants, and 30 centimeters between rows. Every tenth row was a parent of each respective cross where their F3 lines occurred.

Fertilizer was applied at the rate of 100 kg ha^{-1} of nitrogen and 40 kg ha^{-1} of phosphorous prior to planting. And additional 50 kg ha^{-1} of nitrogen was applied at the early tillering growth stage. Weeds were controlled by hand and with a preemergence applications of Paraquat (1.0 lt ha^{-1}).

The experimental plots were artificially inoculated with $5x10^6$ to $8x10^6$ spores per millimeter of suspension of the virulent Septoria tritici isolate identified as C-33. The isolate C-33 was obtained from Dr. L. Gilchrist (CIMMYT, Plant Pathology Program) and was isolated from a single pycnidium in an infected wheat plant from a nursery grown in Patzcuaro, Michoacan, Mexico.

Inoculum preparation and application were carried out following recommendations by Eyal et al., (1987). Inoculation was initiated when early maturing parents reached the growth stage where the third node was detectable and terminated when the late maturing parents reached spike emergence.

A. Collection of Data

Fifty randomly selected plants from each parent, 25 plants from each F1, and 400 plants from each F2 population were evaluated. For the parents and F3 lines in the split plot design five plants were analyzed from each family. The following information was obtained:

1. Heading Date (HD) was recorded when three spikes on the plant appeared.
2. Plant Height (PHGT) was measured in centimeters (cm) from the ground to the tip of the tallest spike of the plant.
3. Percent of Septoria infection on Flag Leaf (SEPFL). Septoria tritici severity readings were made on the flag leaf when early maturing parents reached the milk stage of growth (stage 73 on Zadoks scale). For each individual plant all flag leaves were visually inspected. Only the single most infected flag leaf on each plant was scored.
4. Relative Coefficient of Infection (RCI). A double digit (00-99) scale was used to calculate the intensity of infection of Septoria tritici. The first digit represents vertical disease progress and the second value a severity estimate.
5. Septoria Progress Coefficient (SPC):

$$SPC = \text{Disease Height (cm)} / \text{Plant Height (cm)},$$

where: Disease Height = the maximal height (cm) above the ground level at which the pycnidia of Septoria tritici could be found on the plant tissue.

B. Statistical and Genetic Analysis

Data on S. tritici were analyzed on a single plant basis. To test the null hypothesis that there were no genotypic differences among the parents, F1 and F2 populations, an analysis of variance for a completely randomized design was used (Steel and Torrie, 1981). For the parents and F3 lines a randomized block analysis was employed.

General combining ability (GCA) and specific combining ability (SCA) variances were computed according to the model I, method 4 of Griffing (1956). Model I is a fixed model. Method 4, includes one set of F1 crosses, but neither parents nor reciprocals F1s. The statistical model is:

$$Xij = u + gi + gj + si$$

Where:

u = The population mean.

gi = The GCA effect of parent i.

gj = The GCA effect of parent j.

si = The SCA effect for the combination of parent i and j.

The restrictions sum gi= 0 and sum si= 0 are imposed on the combining ability effects. Overall means of all F1 plants were used to estimate the general combining ability (GCA) and specific combining ability (SCA) variance components, and the individual combining ability effects. A similar diallel analysis was carried out for the F2 and F3 generations.

To test the GCA and SCA effect:

$F = [(p - 1), m] = MSg/MSe$; and

$F = [p (p - 3)/2, m] = MSs/MSe$

Where:

p = The number of parents

m = The degree of freedom associated with the error

MSg = Mean square of the GCA

MSs = Mean square of the SCA

MSe = Mean square of the error

F = 'F' test

Gene action was estimated from the variance components of general and specific combining ability using the method described by Griffing (1956).

Heritability in narrow sense was calculated from the diallel analysis estimates of genetic variance using the formula described by Suzuki et al (1980).

$h^2_n = \sigma^2_A / \sigma^2_P$

$\sigma^2_P = \sigma^2_A + \sigma^2_D + \sigma^2_E$

where:

h^2_n = Heritability estimate in the narrow sense

σ^2_A = Additive genetic variance

σ^2_P = Phenotypic variance

σ^2_D = Dominance + epistatic variance

σ^2_E = Environmental variance

Narrow-sense heritability for the F3 generation was estimated using the following formula described by Das (1990):

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

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

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

where:

σ^2_g = Genetic variance

σ^2_L = Variance among the F3 populations, which is obtained from the treatment mean square.

σ^2_E = Error variance

r = number of replications

Phenotypic correlation coefficients were calculated to evaluate probable relationship for each factor studied using the following formula described by Suzuki et al (1980).

$$r = CovXY/\sqrt{(\sigma^2X)(\sigma^2Y)}$$

Where:

CoVXY = Covariance of the two factors under study

σ^2X = Phenotypic variance of the factor X under study

σ^2Y = Phenotypic variance of the factor Y under study

Genetic correlation coefficients were calculated to evaluate probable heritable relationship for all of the disease traits using the following formula described by Burton (1951):

$$Genetic\,r = (CovXYF2 - CovXYF1)/\sqrt{(\sigma^2XF2 - \sigma^2XF1)(\sigma^2YF2 - \sigma^2YF1)}$$

Where:

CovXYF2 = Covariance of F2 of the two factors under study

CovXYF1 = Covariance of F1 of the two factors under study

σ^2XF2 = Variance of F2 of the factor X under study

σ^2XF1 = Variance of F1 of the factor X under study

σ^2YF2 = Variance of F2 of the factor Y under study

σ^2YF1 = Variance of F1 of the factor Y under study

RESULTS

This study was conducted to investigate the mode of inheritance of selected wheat genotypes observed to have more durable resistance to Septoria tritici. Also the possible association between disease severity measurements and their relationship with heading date and plant height was investigated. The results are presented in two sections. These included a statistical evaluation and a genetic analysis obtained for the five traits from a 4x4 diallel cross involving parents, F1, F2, and F3 generations. Statistical analysis of variance including means, standard deviations, midparent and range values were obtained for the traits Septoria Progress Coefficient, Relative Coefficient of Infection, Septoria Flag Leaf Severity, Heading Date, and Plant Height. The genetic analysis included quantitative evaluation based on the frequency distribution noted in the F2 and F3 generation for the disease traits. Also, information on the nature of the gene action using narrow-sense heritability and combining ability analysis were estimated. Finally, possible associations between the disease traits and plant height and heading date were also examined.

A. Statistical Analysis

I. Evaluation of Parental Performance

Observed mean squares among the parents for the five traits are presented in Table 1. Significant differences were found for all measured traits. The coefficients of variation values were intermediate for Septoria progress coefficient and Relative coefficient of infection, high for Septoria flag leaf severity, and low for heading date and plant height.

Parental mean values and standard deviations for the five traits are provided in Table 2. Tukey studentized range test was performed and differences among parents were observed for most traits, with all four parents plant height being the one exception. Bobwhite "S" showed lowest mean values for Septoria progress coefficient, Relative coefficient of infection, and Septoria flag leaf severity. These values were slightly higher for Kavkaz/K4500 L.A.4 . Oasis/Torim ranked third with intermediate values while Ciano 79 was the most susceptible and had higher values for the disease traits. Differences for heading date were also present with Ciano 79 being the earliest and Oasis/Torim the latest. Differences in plant height were also observed for most parents, except for Bobwhite "S" and Ciano 79, which were similar and the shortest parental lines. The tallest parent was Kavkaz/K4500 L.A.4 .

II. Evaluation of F1 Generation Performance

Observed mean squares among the F1 generation from 4x4 diallel for the five traits are presented in Table 3. Significant differences were found for all traits. Coefficients of variation values were high for Septoria flag leaf severity, intermediate for Septoria progress coefficient and Relative coefficient of infection, and low for Heading date and Plant height.

Table 1. Observed mean square and coefficient of variation for Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) for four parents grown at CODAGEM, Toluca, Mexico, 1989.

		Mean Squares				
Source of Variation	df	SPC	RCI (%)	SEPFL (%)	HD (days)	PHGT (cm)
BLOCK	2	0.0011	7.73	137.07	2.15	1.82
GENOTYPE	3	5.6640**	41551.82**	107141.51**	4662.97**	3677.43**
ERROR	6	0.0036	10.41	17.51	0.7558	0.7813
C.V. (%)		12.94	14.64	19.15	1.07	2.11

** Significant at the 0.01 probability level

Table 2. Mean and standard deviation values for Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) of four parents grown at CODAGEM, Toluca, Mexico, 1989.

	Means and Standard Deviations				
Genotype	SPC	RCI (%)	SEPFL (%)	HD (days)	PHGT (cm)
BOW "S"	0.29±0.07 a†	17.27±5.49 a	2.43±4.60 a	81.2±0.39 b	80.0±0.00 a
KVZ/K450	0.40±0.07 b	27.68±7.47 b	21.04±11.19 b	86.2±1.16 c	94.9±0.59 c
OAS/TRM	0.71±0.09 c	50.41±6.49 c	58.19±10.39 c	93.0±0.37 d	87.9±3.34 b
CIANO 79	0.90±0.05 d	71.06±4.16 d	88.89±3.17 d	74.0±1.27 a	80.1±1.18 a

† Tukey studentized range test; means in the same column having the same letter are not significantly different at the 0.05 probability level
Bow = Bobwhite "S", Kvz/K4500 = Kavkaz/K4500 L.A.4,
Oas/Trm = Oasis/Torim.

Means, standard deviations for the F1's, and midparent values for the five traits are presented in Appendix Table 1 to 5. Tukey studentized range test showed significant differences among F1 crosses. Consistently low mean values for Septoria progress coefficient, Relative coefficient of infection, and Septoria flag leaf severity were observed for the F1's from Bobwhite "S"//Kavkaz/K4500 L.A.4 , Bobwhite "S"/Ciano 79, and Kavkaz/K4500 L.A.4//Oasis/Torim. The F1 populations involving the parent Oasis/Torim consistently showed the highest mean values for these traits. The mean values for the three disease traits in the F1's were lower than susceptible parent Ciano 79 (Appendix Table 1 to 3).

Differences in heading date among the F1 populations were small, except for the cross Bobwhite "S"/Ciano 79, which was the earliest. In contrast, the F1 crosses involving the parent Oasis/Torim had the highest mean values for this trait. Highest means for heading date were observed in F1 populations obtained from crosses involving resistant x susceptible parents. Crosses involving resistant x resistant parents expressed low means values for heading date when compared to the midparent values (Appendix Table 4).

Among the F1 populations the cross Bobwhite "S"/Ciano 79 was the shortest, with Kavkaz/K4500 L.A.4//Oasis/Torim being the tallest. All F1 populations were taller than the parents.

III. Evaluation of F2 Generation Performance

Observed mean squares among the F2 generation for the five traits are

Table 3. Observed mean square and coefficient of variation for Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) for F1 generation grown at CODAGEM, Toluca, Mexico, 1989.

		Mean Squares				
Source of Variation	df	SPC	RCI (%)	SEPFL (%)	HD (days)	PHGT (cm)
F1	5	0.0868**	771.12**	5861.87**	140.29**	1653.10**
ERROR	144	0.0099	55.15	153.61	0.1538	0.8572
TOTAL	149					
C.V. (%)		17.53	18.09	30.18	0.47	1.0

** Significant at the 0.01 probability level

presented in Table 4. Significant differences were found for all traits. Coefficients of variation values were high for Septoria progress coefficient, Relative coefficient of infection, and Septoria flag leaf severity, intermediate for Plant height, and low for Heading date.

Means, standard deviations, and ranges of values for the five traits measured for the six crosses are presented in Appendix Tables 6 to 10. Tukey studentized range test was performed for the five traits where differences among F2 populations were observed. The estimates measured in Appendix Tables 6, 7, and 8 indicate that the cross Bobwhite "S"//Kavkaz/K4500 L.A.4 showed the lowest mean values for Septoria progress coefficient, Relative coefficient of infection, and Septoria flag leaf severity in the F2 generation. As these lines also had the lowest values individually. However, of the 400 plants studied in F2 populations, from this cross susceptible segregates were noted, indicating that the parents carry different genes. In general the F2 populations involving the parent Oasis/Torim gave the highest mean values for these traits. All of the F2 crosses involving resistant x resistant (i.e. Bobwhite "S"//Kavkaz/K4500 L.A.4, Bobwhite "S"//Oasis/Torim, and Kavkaz/K4500 L.A.4 //Oasis/Torim) had progenies with higher susceptibility values than either parent. Also progenies were noted to have lower values than either parents as well.

Differences for heading date among the F2 populations were small, except for the cross Kavkaz/K4500 L.A.4/Ciano 79 which had the earliest heading date. The F2 populations involving the parent Oasis/Torim presented the highest mean

Table 4. Observed mean square and coefficient of variation for Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) for F2 generation grown at CODAGEM, Toluca, Mexico, 1989.

		Mean Squares				
Source of Variation	df	SPC	RCI (%)	SEPFL (%)	HD (days)	PHGT (cm)
F2	5	5.89**	21556.82**	327069.66**	2364.54**	16401.04**
ERROR	2394	0.035	203.83	560.66	29.01	180.87
TOTAL	2399					
C.V. (%)		29.40	31.33	59.20	6.47	15.58

** Significant at the 0.01 probability level

values for this trait (Appendix Table 9).Among the F2 populations variability for plant height was also present. The cross Bobwhite "S"//Oasis/Torim was the shortest, with the cross Kavkaz/K4500 L.A.4//Oasis/Torim progeny being the tallest (Appendix Table 10).

IV. Evaluation of F3 Generation Performance

Observed mean squares among the F3 generation for the traits measured are presented in Table 5. Significant differences were found for all traits. Coefficient of variation values were moderate for Septoria progress coefficient, Relative coefficient of infection, and Septoria flag leaf severity, and low for Heading date and Plant height.

Means, standard deviations, and ranges values for the five traits measured are presented in Appendix Table 11 to 15. Tukey studentized range test was performed for the five traits where differences among F3 populations were observed. The performance of F3 populations of the cross Bobwhite "S"//Kavkaz /K4500 L.A.4 on the average was again lowest confirming the values noted in F2 generation. The means values for the lines from this cross ranked from 0.22 - 0.90, 9.88 - 69.14, and 00.0 - 80.0 for Septoria progress coefficient, Relative coefficient of infection, and Septoria flag leaf severity respectively. These values were lower and higher for the three disease traits when compared to the parents, showing transgressive segregation. The highest values for these traits was obtained for the F3 lines from the parent Oasis/Torim (Appendix Table 11 to 13) which was

Table 5. Observed mean square and coefficient of variation for Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) for F3 generation grown at CODAGEM, Toluca, Mexico, 1989.

		Mean Squares				
Source of Variation	df	SPC	RCI (%)	SEPFL (%)	HD (days)	PHGT (cm)
BLOCK	2	0.2318	1199.68	1118.25	61.78	300.76
CROSS(C)	5	1.5971**	15048.73**	37543.06**	1372.49**	3836.89**
ERROR(A)	10	0.0129	73.37	193.84	2.43	62.65
LINES(L)	63	0.0987**	607.51**	1803.27**	37.82**	406.94**
C x L	315	0.0887**	563.15**	1526.20**	39.52**	374.75**
ERROR(B)	126	0.0042	26.39	43.44	0.65	10.95
TOTAL	1151					
C.V. (%)		11.69	11.61	17.82	0.99	3.69

** Significant at the 0.01 probability level

also true in the F2 generation. Differences for heading date among the F3 lines were small. The F3 populations involving Ciano 79 had the lowest mean values for heading date in all F3 lines where it was a parent (Appendix Table 14).

Among the F3 lines, variability in plant height was present. Although differences between crosses were small, the plant height within the F3 lines for a cross was large. Bobwhite "S" //Oasis/Torim and Bobwhite "S"/Ciano 79 F3 lines were the shortest, while the cross Kavkaz/K4500 L.A.4//Oasis/Torim resulted in the tallest progeny (Appendix Table 15).

B. Genetic Analysis

I. Frequency Distribution

Resistant x Susceptible Parents

Frequency distributions and means of the three disease traits in crosses between resistant x susceptible involving parents, F1, F2, and F3 generation are presented in the Appendix Tables 16 to 18. A continuous distribution of the F2 populations were observed for Septoria progress coefficient, Relative coefficient of infection, and Septoria flag leaf severity. This Suggests that the inheritance for these traits was quantitative, as it was not possible to classify plants into discrete classes (Figures 1 to 9).

Frequency distributions involving parents, F2, and F3 generations from the cross between the resistant parent Bobwhite "S" and the susceptible parent Ciano 79 are presented in the Figures 1 to 3. The distribution of the F2 appears normal for all disease traits, except for Septoria flag leaf severity. Plant types were recovered with reactions similar to both parents for Septoria progress coefficient and Relative coefficient of infection traits. For Septoria flag leaf severity, a tendency to recover more resistant plant types is apparent. This suggests that resistance to Septoria tritici on flag leaves has a partialy dominant effect in Bobwhite "S" (Figure 3). The F3 frequency distribution for this cross showed similar patterns for the three disease traits.

Similar results were also observed in the F2 and F3 mean values for the cross between the resistant parent Kavkaz/K4500 L.A.4 and the susceptible parent Ciano 79 (Figure 4 to 6). Transgressive segregation towards resistance occurred for Septoria progress coefficient in the F3 generation (Figure 4).

In the cross between the resistant parent Oasis/Torim and the susceptible parent Ciano 79 resistance appeared to be partialy dominant. There was however, a tendency in this cross to show higher infection values in the F2 and F3 populations (Figure 7 to 9). Transgressive segregation towards resistance was again found in the F2 and F3 for the three disease traits.

Resistant x Resistant Parents

Frequency distributions and means of Septoria progress coefficient, Relative coefficient of infection, and Septoria flag leaf severity in crosses between resistant x resistant involving parents, F1, F2, and F3 generations are presented in Appendix Tables 19 to 21. Distribution of the F2 populations were observed to be continuous for the three disease traits. Therefore, an attempt to do qualitative analysis in the F2 and F3 generations was impossible due to lack of clear discrete classes segregation for all three crosses and three traits.

Frequency distribution from the cross between Bobwhite "S" and Kavkaz/K4500 L.A.4 showed that the mean of the F2 were higher in all disease traits. Transgressive segregation towards resistance and susceptibility occurred for Septoria progress coefficient (Appendix Table 19). The F3 frequency distribution for this cross showed similar patterns for the three disease traits. However, transgressive segregation was greater for susceptibility for all disease traits. The data in the Appendix Tables 19 to 21 suggests that this relationship continued to hold in crosses between Bobwhite "S" and Oasis/Torim and Kavkaz/k4500 L.A.4 and Oasis/Torim among the F2 and F3 populations. This indicated that genes for resistance to S. tritici among the resistant parents are different.

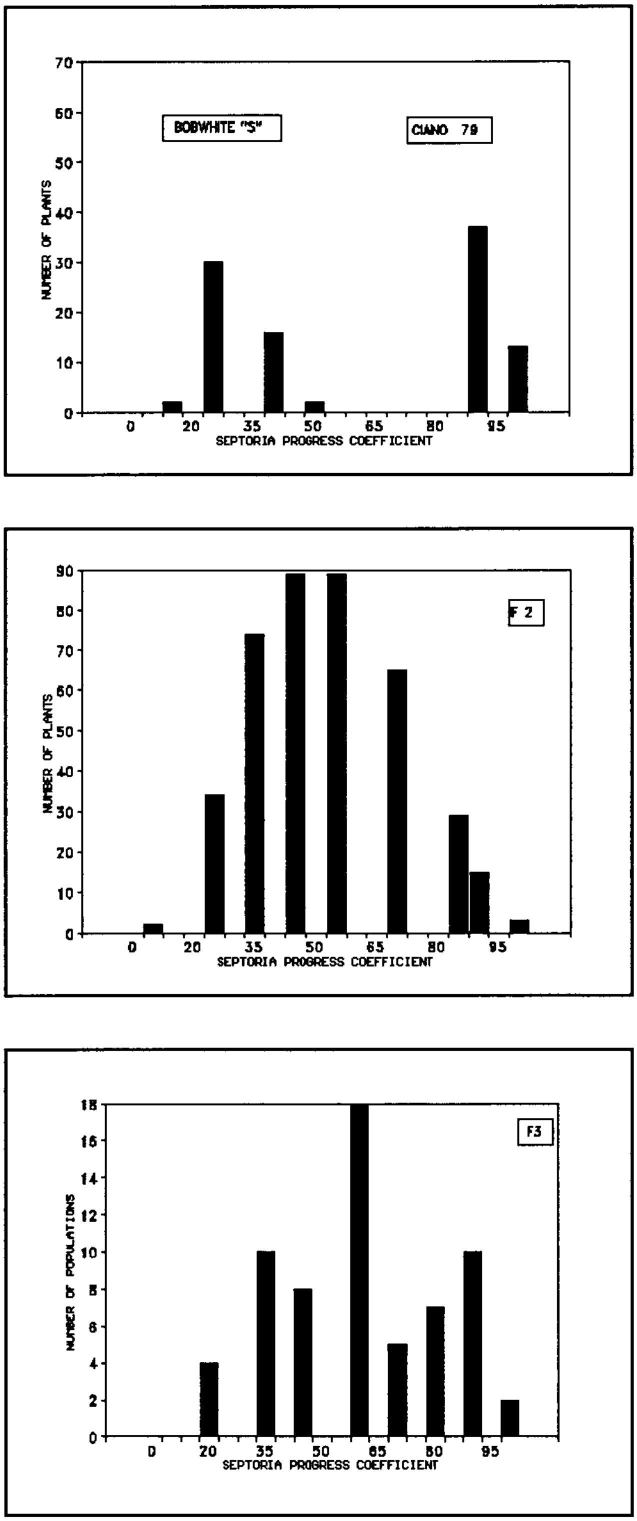


Fig. 1. Frequency distribution (number of plants and populations) of Septoria progress coefficient (SPC) of parents, F2, and F3 generations from the cross Bobwhite "S"/Ciano 79 grown at CODAGEM, Toluca, Mexico, 1989.

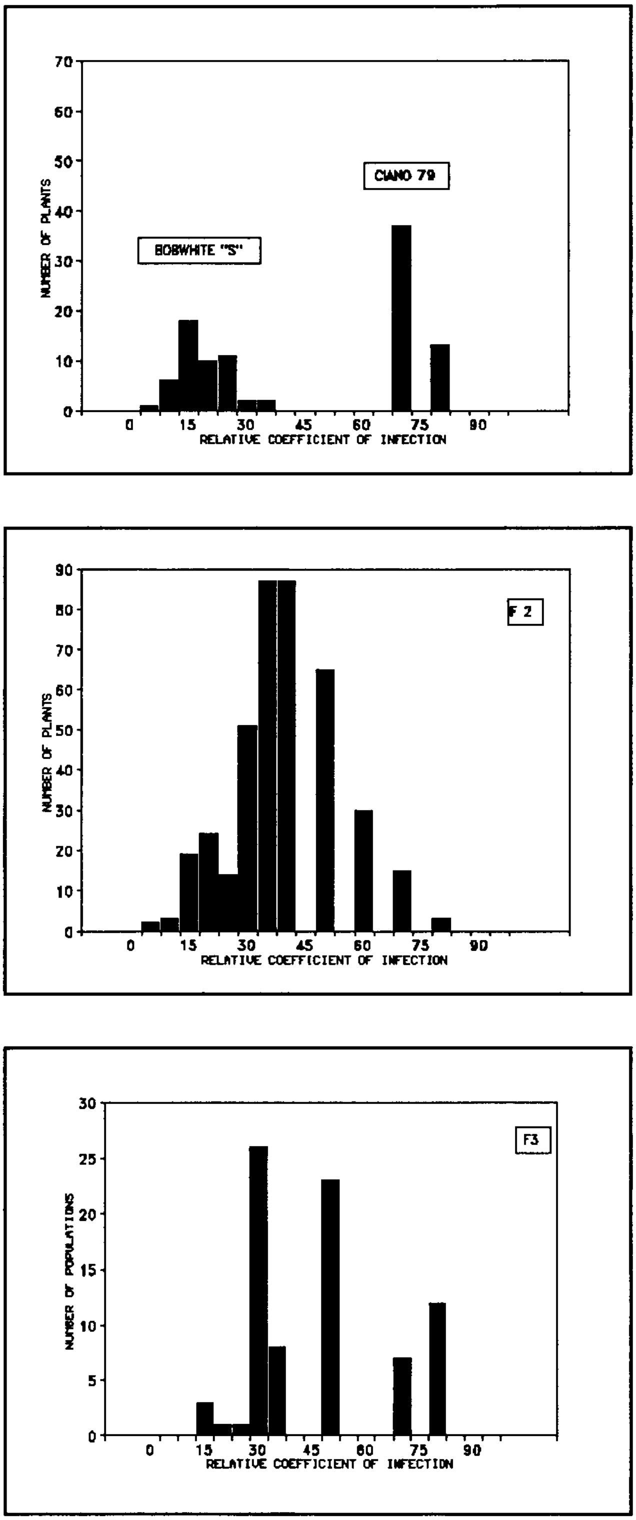


Fig. 2. Frequency distribution (number of plants and populations) of Relative coefficient of infection (RCI) of parents, F2, and F3 generations from the cross Bobwhite "S"/Ciano 79 grown at CODAGEM, Toluca, Mexico, 1989.

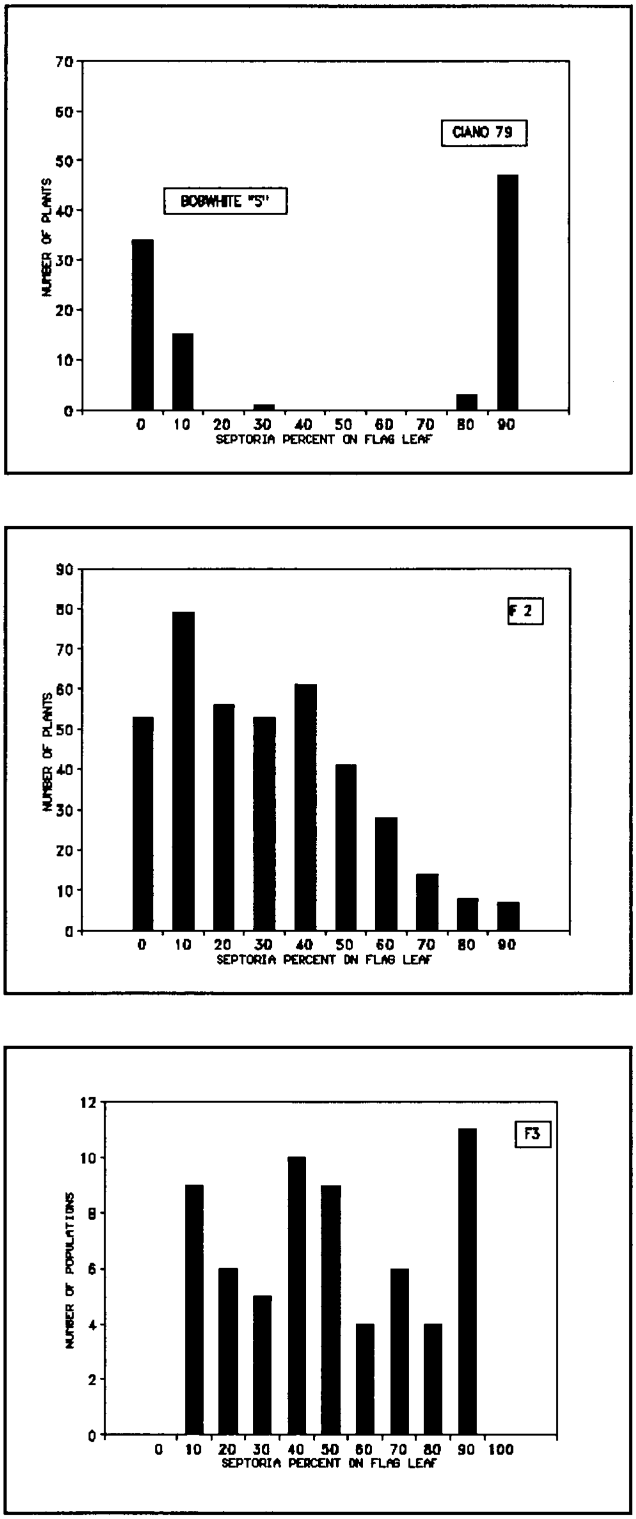


Fig. 3. Frequency distribution (number of plants and populations) of Septoria flag leaf (SEPFL) of parents, F2, and F3 generations from the cross Bobwhite "S"/Ciano 79 grown at CODAGEM, Toluca, Mexico, 1989.

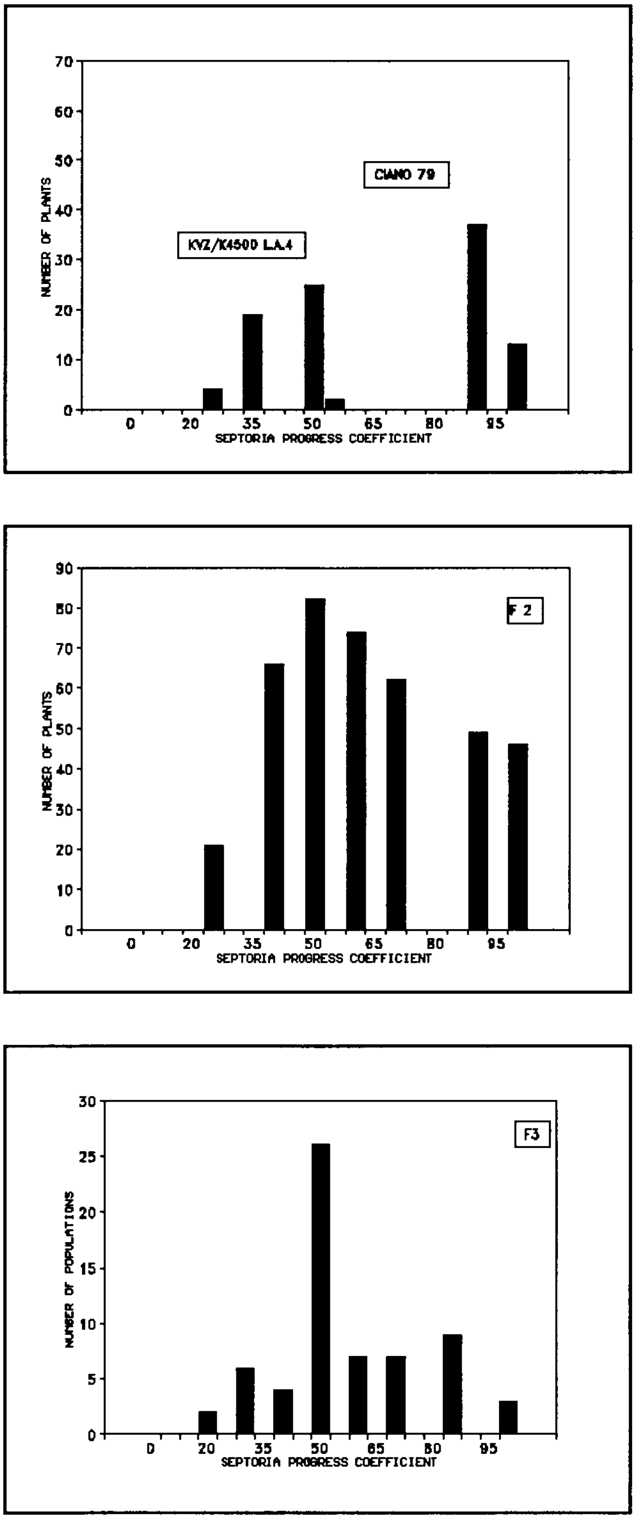


Fig. 4. Frequency distribution (number of plants and populations) of Septoria progress coefficient (SPC) of parents, F2, and F3 generations from the cross Kavkaz/K4500 L.A.4/Ciano 79 grown at CODAGEM, Toluca, Mexico, 1989.

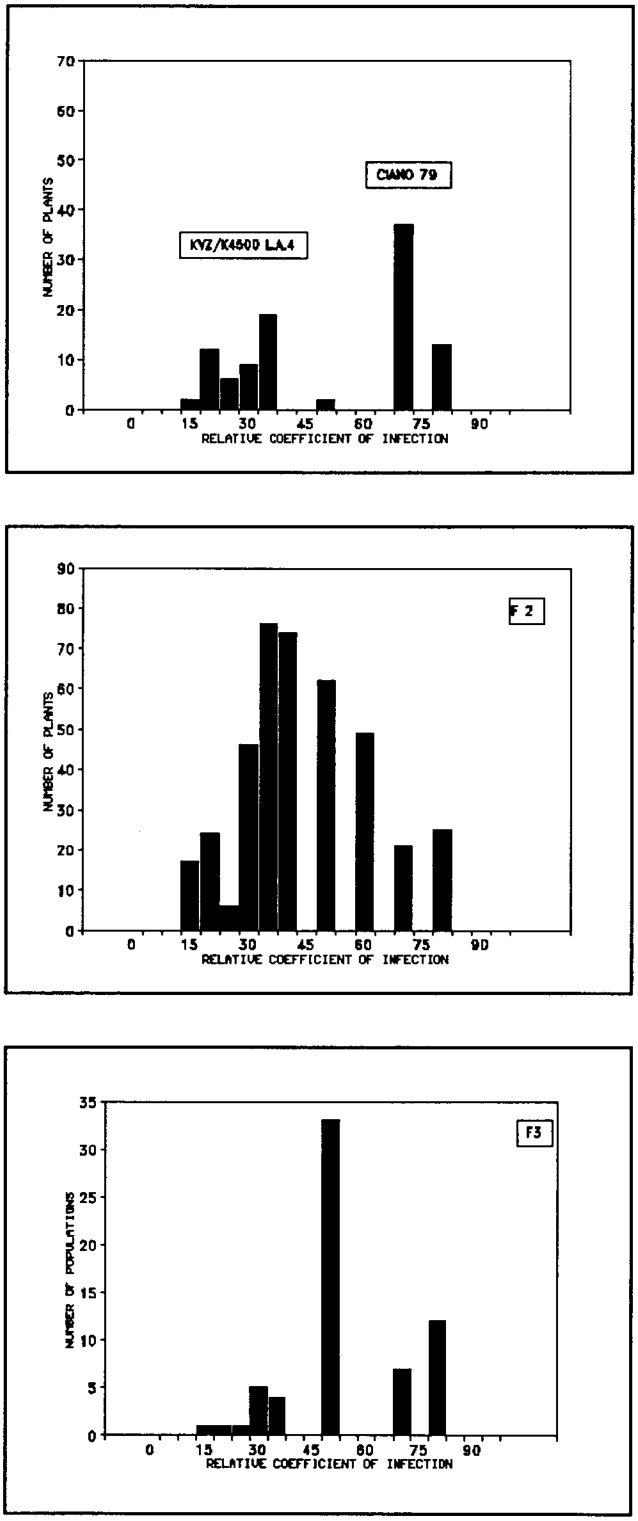


Fig. 5. Frequency distribution (number of plants and populations) of Relative coefficient of infection (RCI) of parents, F2, and F3 generations from the cross Kavkaz/K4500 L.A.4/Ciano 79 grown at CODAGEM, Toluca, Mexico, 1989.

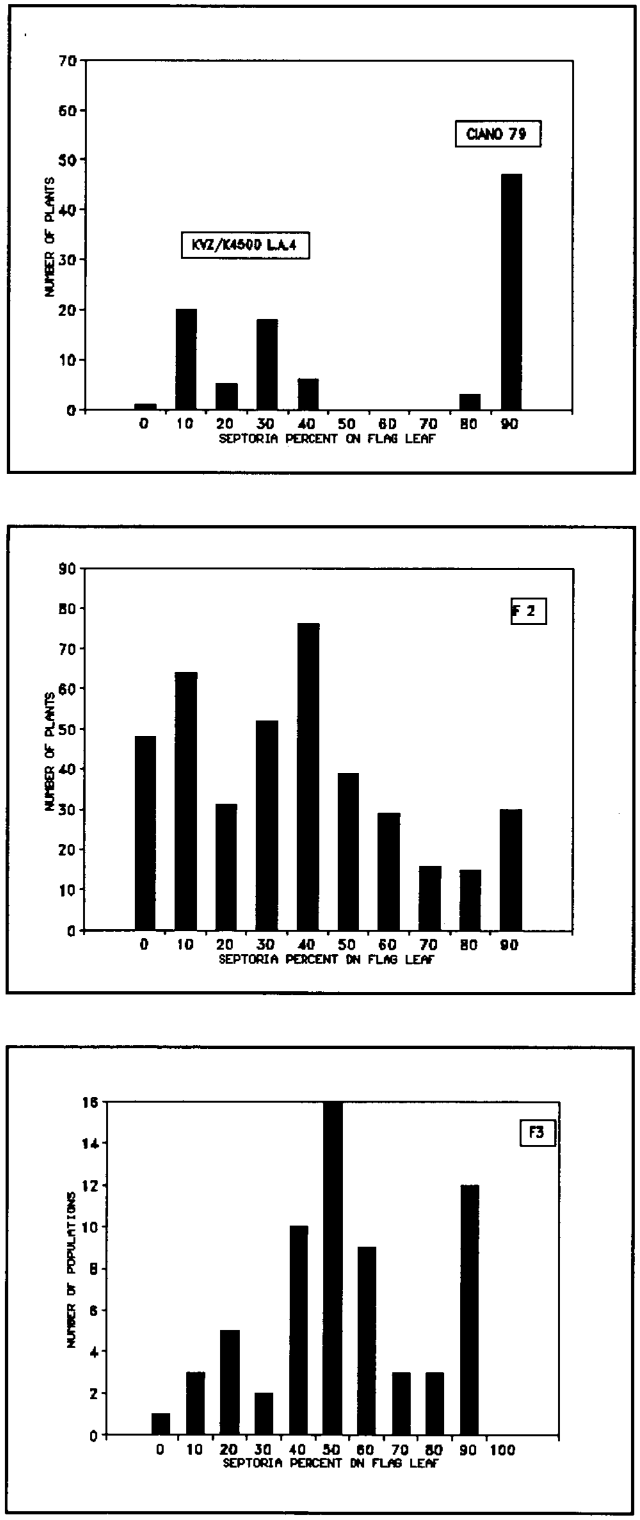


Fig. 6. Frequency distribution (number of plants and populations) of Septoria flag leaf (SEPFL) of parents, F2, and F3 generations from the cross Kavkaz/K4500 L.A.4/Ciano 79 grown at CODAGEM, Toluca, Mexico, 1989.

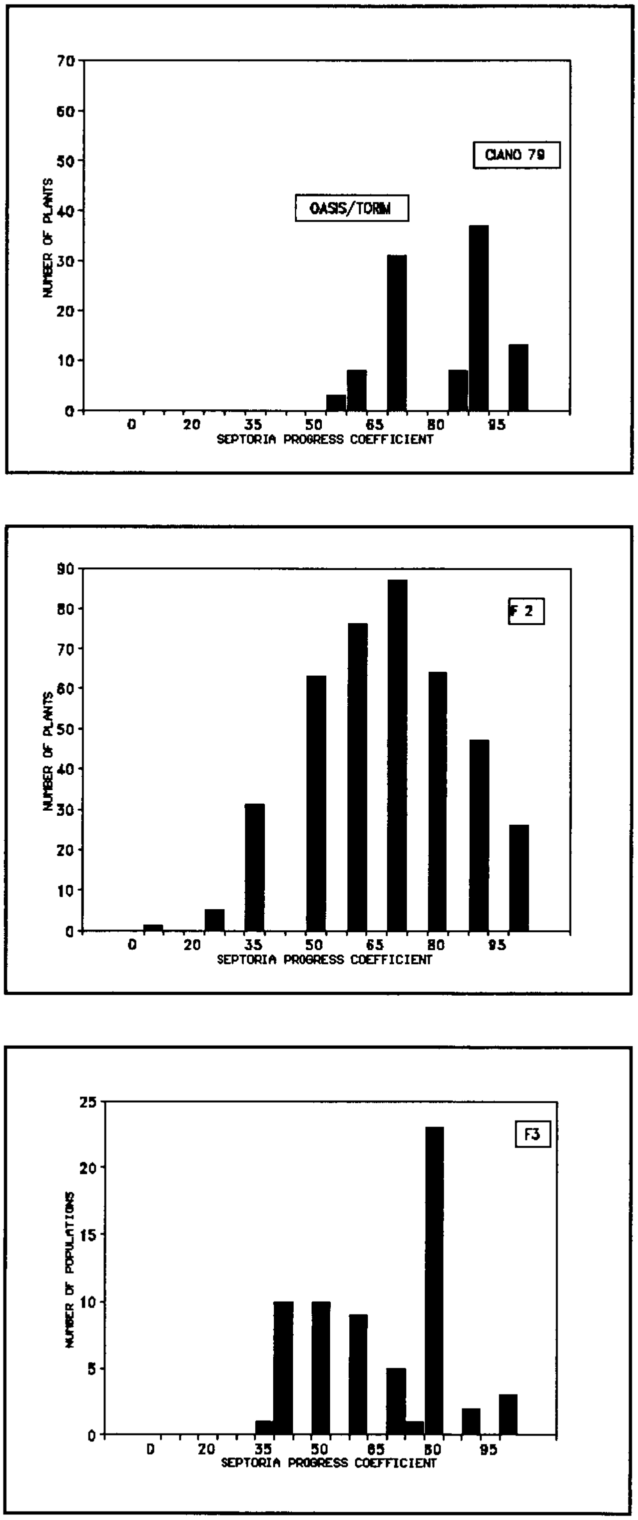
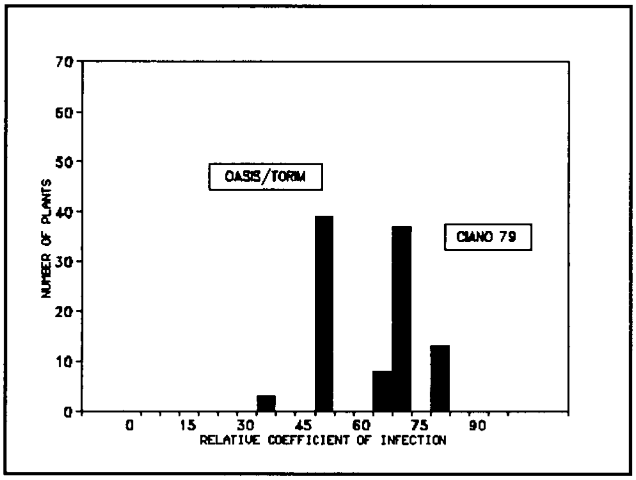
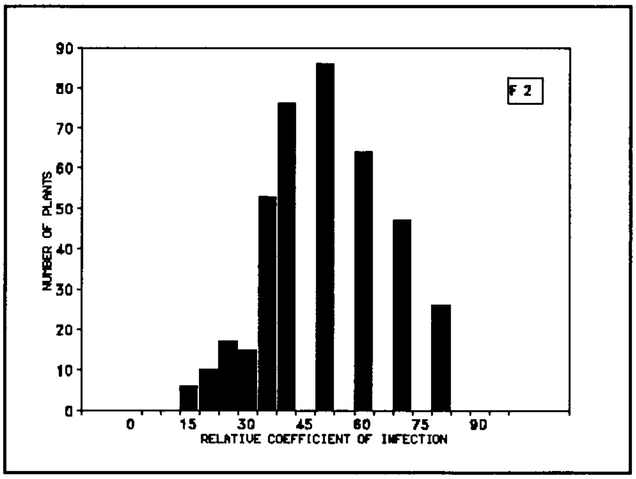


Fig. 7. Frequency distribution (number of Plants and populations) of Septoria progress coefficient (SPC) of parents, F2, and F3 generation from the cross Oasis/Torim//Ciano 79 grown at CODAGEM, Toluca, Mexico, 1989.





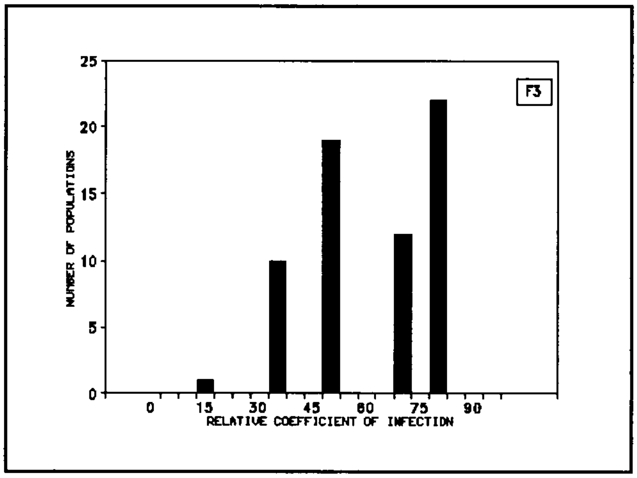


Fig. 8. Frequency distribution (number of Plants and populations) of Relative coefficient of infection (RCI) of parents, F2, and F3 generation from the cross Oasis/Torim//Ciano 79 grown at CODAGEM, Toluca, Mexico, 1989.

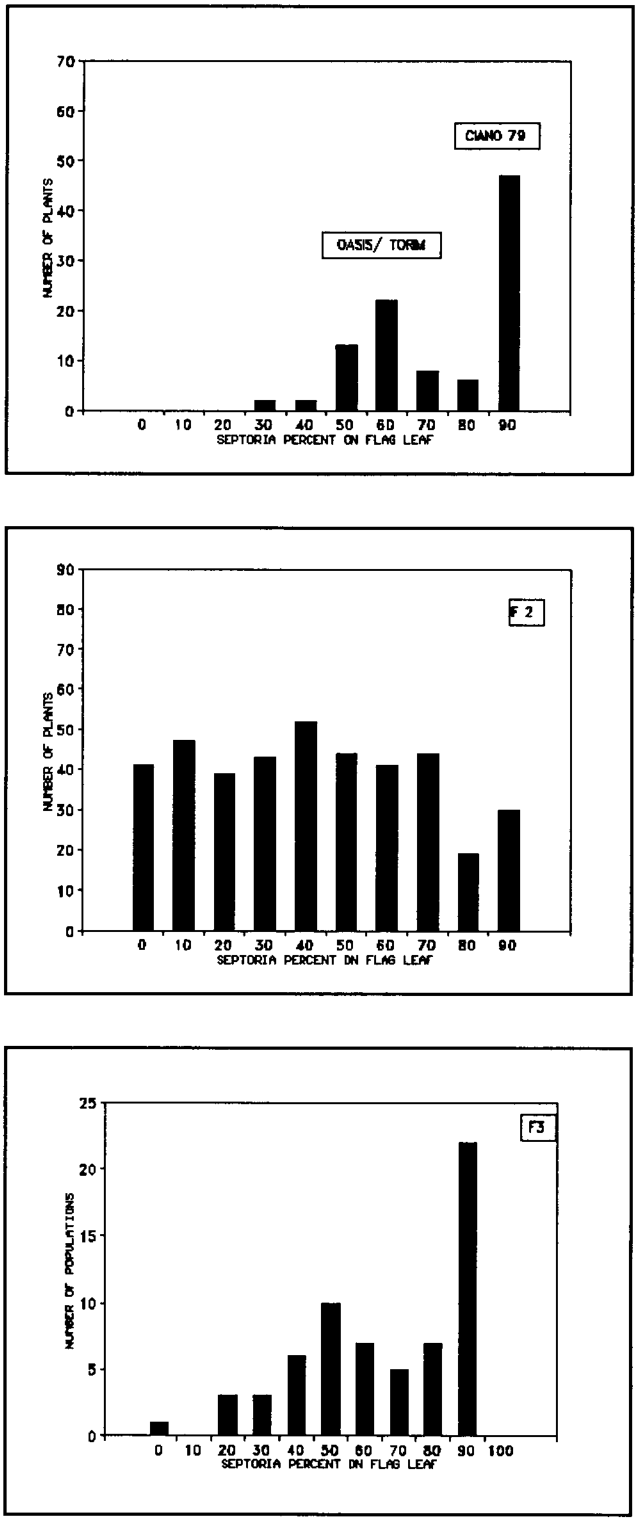


Fig. 9. Frequency distribution (number of Plants and populations) of Septoria flag leaf (SEPFL) of parents, F2, and F3 generation from the cross Oasis/Torim//Ciano 79 grown at CODAGEM, Toluca, Mexico, 1989.

II. Nature of Gene Action

As differences among F1, F2 and F3 populations were highly significant, combining ability analysis was used to estimate the nature of the gene action controlling the disease traits measured. General combining ability (GCA) involves mainly additive gene action effects. The specific combining ability (SCA) estimates the deviation of the crosses from the value expected on the basis of the performance of the parents, and involves the nonadditive gene action effects (Griffing, 1956).

Evaluation of F1 Generation

General and specific combining ability analysis for the F1 generations for the five traits measured are presented in Table 6. Both GCA and SCA mean squares were significant for these traits. However, the ratio of GCA/SCA was high, suggesting that a large part of the genetic variability was associated with additive effects for all of the traits.

Genetic components of variance estimated for the disease traits are presented in the Table 7. Genetic estimates showed that σ^2 GCA components exceeded σ^2 SCA components in values for Septoria progress coefficient and Septoria flag leaf severity. This confirmed a greater importance of additive type of inheritance for these traits. However, the genetic components of variance for Relative coefficient of infection were almost equal for σ^2 SCA and σ^2 GCA, indicating that both additive and nonadditive effects were of equal importance.

Table 6. Observed mean square for General Combining Ability (GCA) and Specific Combining Ability (SCA) for Septoria coefficient progress (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) involving the F1 from a 4x4 diallel cross when grown at CODAGEM, Toluca, Mexico, 1989.

		Mean Squares				
Source	df	SPC	RCI	SEPFL	HD	PHGT
GCA	3	0.005767**	40.85**	335.52**	8.41**	110.09**
SCA	2	0.000039**	15.84**	82.90**	1.41**	0.17**
ERROR	144	2.76E-06	2.21	0.000427	4.27E-05	2.38E-04
GCA/SCA		145.5	2.58	4.05	5.95	634.17

** Significant at the 0.01 probability level

Table 7. Estimates of genetic variance for Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), and Septoria flag leaf severity (SEPFL) involving the F1 from a 4x4 diallel cross when grown at CODAGEM, Toluca, Mexico, 1989.

	Estimates Values		
Variance Component	SPC	RCI	SEPFL
σ^2 GCA	0.002864	12.50464	126.3061
σ^2 SCA	0.0000369	13.63385	82.9062
σ^2_A	0.005727	25.00928	252.6133
σ^2_E	0.009951	55.14609	1.5361

Evaluation of F2 Generation

General and specific combining ability analysis for the F2 populations involving the five traits measured are provided in Table 8. Differences in both GCA and SCA were observed for all of the traits. The GCA/SCA ratio was low for Septoria progress coefficient and Septoria flag leaf severity, and high for Relative coefficient of infection. This suggests that nonadditive effects were playing an important role in the expression of Septoria leaf blotch for these traits. This is supported also by the genetic components of variance that were nearly equal for σ^2 GCA and σ^2 SCA for Septoria progress coefficient and Septoria flag leaf severity. While GCA estimates were found higher for Relative coefficient of infection. This indicates that the variation of the genotypes were associated in equal importance for both additive and nonadditive effects for Septoria progress coefficient and Septoria flag leaf severity; while the expression of Relative coefficient of infection was more influenced by additive gene effects (Table 9).

Evaluation of F3 Generation

Combining ability analysis calculated from F3 populations are presented in Table 10. Differences for both GCA and SCA were observed for all traits involved. The GCA/SCA ratio was high for all of the traits measured.

Genetic estimates showed that σ^2 GCA components exceeded the σ^2 SCA components for all of the disease traits (Table 11). This demonstrate again in this

Table 8. Observed mean square for General Combining Ability (GCA) and Specific Combining Ability (SCA) for Septoria coefficient progress (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) involving the F2 from a 4x4 diallel cross when grown at CODAGEM, Toluca, Mexico, 1989.

Source	df	Mean Squares				
		SPC	RCI	SEPFL	HD	PHGT
GCA	3	0.0197**	80.27**	119.45**	8.76**	66.15**
SCA	2	0.0073**	14.34**	67.18**	1.64**	3.27**
ERROR	2394	3.7E-08	2.13E-04	5.9E-06	3.03E-05	1.9E-04
GCA/SCA		2.73	5.59	2.97	5.33	20.19

** Significant at the 0.01 probability level

Table 9. Estimates of genetic variance for Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), and Septoria flag leaf severity (SEPFL) involving the F2 from a 4x4 diallel cross when grown at CODAGEM, Toluca, Mexico, 1989.

Variance Component	Estimates Values		
	SPC	RCI	SEPFL
σ^2 GCA	0.006269	32.9664	66.1339
σ^2 SCA	0.007219	14.3363	67.1832
σ^2_A	0.012538	65.9328	132.2679
σ^2_E	0.034969	203.8274	5.6066

generation that additive gene effects are more important than nonadditive in determining the expression of resistance to Septoria tritici.

Estimates of GCA effects of each parent are presented in Table 12. Negative values indicate a contribution towards resistance. The resistant parents Bobwhite "S" and Kavkaz/K4500 L.A.4 had the largest negative GCA effects for all disease traits. The parent Oasis/Torim showed higher and intermediate positive GCA effects to Septoria progress coefficient, Septoria flag leaf severity and Relative coefficient of infection respectively. This indicated moderate inheritance of resistance. The susceptible parent Ciano 79 had the highest positive GCA effect values.

Generally, the magnitude and sign of the GCA effects of each parent were in agreement with their individual performance under field conditions.

Table 10. Observed mean square for General Combining Ability (GCA) and Specific Combining Ability (SCA) for Septoria coefficient progress (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) involving the F3 from a 4x4 diallel cross when grown at CODAGEM, Toluca, Mexico, 1989.

		Mean Squares				
Source	df	SPC	RCI	SEPFL	HD	PHGT
GCA	3	0.0114**	124.55**	307.69**	11.22**	29.99**
SCA	2	0.0036**	9.13**	27.38**	1.04**	4.96**
ERROR	192	1.89E-06	0.038	0.0646	0.064	0.064
GCA/SCA		3.15	13.65	11.23	10.77	6.05

** Significant at the 0.01 probability level

Table 11. Estimates of genetic variance for Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), and Septoria flag leaf severity (SEPFL) involving the F3 from a 4x4 diallel cross when grown at CODAGEM, Toluca, Mexico, 1989.

	Estimates Values		
Variance Component	SPC	RCI	SEPFL
σ^2 GCA	0.003904	57.7139	140.1572
σ^2 SCA	0.003633	9.0877	20.9139
σ^2_A	0.007808	115.4279	280.3144
σ^2_E	0.012926	73.3684	1.9384

Table 12. Estimates of general combining ability (gi) effects based on the analysis of F3 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

PARENT	(gi) ESTIMATES		
	SPC	RCI	SEPFL
BOBWHITE "S"	-0.0555	-7.340	-10.67
KAVKAZ/K4500 L.A.4	-0.0748	-5.954	-10.61
OASIS/TORIM	0.0645	4.511	8.55
CIANO 79	0.0659	8.783	12.72
S.E gi - gj	0.0014	0.1954	0.25

III. Heritability

Narrow sense heritability estimates were calculated to determine the portion of genotypic variance that can be transmitted to the next generation. Heritability estimates obtained involving the F1, F2, and F3 generations are presented in Table 13.

A consistent tendency for all traits was for the heritability estimates to be higher in the F1 and F3 generation, in contrast to the F2 where the estimates were lower. The highest heritability estimates in the F1 generation were obtained for plant height, followed by heading date. The lowest estimates were observed for the disease traits; however, the estimate for Septoria flag leaf severity was relatively high.

The highest heritability estimate observed in the F2 was for Septoria flag leaf severity. Similar results was obtained for Septoria flag leaf severity in the F3 generation. Estimate values for Septoria progress coefficient and Relative coefficient of infection were low, while for heading date and plant height the values were low.

Narrow-sense heritability estimates based on the five traits, including the six crosses in the F3 generation are presented in Table 14. Estimated values were high for all traits. On average the narrow-sense heritability estimates for the resistant x susceptible crosses were larger than those for resistant x resistant crosses involving the disease traits. The highest values among the six crosses were obtained in heading date, followed by plant height and Septoria flag leaf severity.

Table 13. Narrow-sense heritability for Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) involving the F1, F2, and F3 generation grown at CODAGEM, Toluca, Mexico, 1989.

TRAIT	HERITABILITY F1	F2	F3
SPC	36.4	22.9	51.8
RCI	26.7	23.2	58.33
SEPFL	74.5	64.5	90.5
HD	81.7	18.8	77.7
PHGT	99.1	25.5	78.6

Table 14. Narrow-sense heritability for Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) involving the F3 generation grown at CODAGEM, Toluca, Mexico, 1989.

	HERITABILITY				
CROSS	SPC	RCI	SEPFL	HD	PHGT
Bobwhite "S"//Kavkaz/K4500 L.A.4	76.8	81.1	86.9	94.9	89.3
Bobwhite "S"//Oasis/Torim	80.9	81.1	85.6	91.8	85.3
Bobwhite "S"/Ciano 79	86.1	86.7	88.0	93.3	92.7
Kavkaz/K4500 L.A.4//Oasis/Torim	91.0	91.3	93.2	91.6	93.1
Kavkaz/K4500 L.A.4//Ciano 79	88.0	87.8	89.7	96.8	88.9
Oasis/Torim//Ciano 79	92.2	92.8	95.3	93.9	94.2

IV Phenotypic and Genetic Correlations

Phenotypic correlation coefficients were calculated to examine the association between the disease traits related to Septoria tritici, heading date and plant height. Phenotypic correlations among F2 and F3 populations involving the factors measured are presented in the Table 15, 16, and 17.

Significant high positive phenotypic correlations were obtained in all crosses among the F2 and F3 populations for the three disease traits, with one exception. In the cross Bobwhite "S"//Oasis/Torim, this association was low and negative between Septoria progress coefficient and relative coefficient of infection in the F2 generation.

Significant negative phenotypic correlations were found in all crosses among the F2 populations. Consistently low negative association were observed between disease traits and heading date. Plant height also showed significant negative phenotypic correlations with the three disease traits. However, plant height showed stronger association with Septoria progress coefficient, Relative coefficient of infection, and Septoria flag leaf severity involving the cross Oasis/Torim//Ciano 79 and also with the disease trait Septoria flag leaf severity for the cross Bobwhite "S"/Ciano 79 than heading date.

Significant negative phenotypic correlations were found among the characters measured in the F3 populations, with one exception. Low and moderate negative phenotypic correlations were noted between disease traits and heading date. The crosses Kavkaz/K4500 L.A.4//Ciano 79 and Oasis/Torim//Ciano 79

Table 15. Correlation coefficient among Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), using the F2 and F3 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

	SPC / RCI		SPC / SEPFL		RCI / SEPFL	
CROSS†	F2	F3	F2	F3	F2	F3
BOW//K/K	0.96**	0.98**	0.74**	0.89**	0.78**	0.90**
BOW//OAS/TRM	-0.11*	0.99**	0.56**	0.94**	0.57**	0.94**
BOW/CNO	0.89**	0.99**	0.75**	0.96**	0.85**	0.96**
K/K//OAS/TRM	0.99**	0.99**	0.91**	0.96**	0.91**	0.96**
K/K//CNO	0.99**	0.99**	0.93**	0.96**	0.93**	0.96**
OAS/TRM//CNO	0.99**	0.99**	0.91**	0.94**	0.91**	0.96**

† BOW = Bobwhite "S", OAS/TRM = Oasis/Torim, CNO = Ciano 79, K/K = Kavkaz/K4500 L.A.4

*, **, Significant at the 0.05 and 0.01 probability level

N = Total number of plants in F2: 400, and F3: 192.

showed the strongest association. Plant height also showed a consistent negative phenotypic correlation with the disease traits in all crosses. Some of these crosses such as Bobwhite "S"/Ciano 79, Kavkaz/K4500 L.A.4//Ciano 79 and Oasis/Torim//Ciano 79 exhibited the highest phenotypic correlations. Although plant height showed the same negative phenotypic association among disease traits for both F2 and F3, the phenotypic correlation values were high in the F3 populations than the F2 populations.

Genetic correlation coefficients were also calculated to examine how much the associations between the disease traits related to Septoria leaf blotch, heading date and plant height were heritable. Negative genetic correlations were found in all crosses among the F2 population (Appendix Table 22). Low negative associations were observed between the disease traits and heading date. Plant height showed high and moderately negative associations between the disease traits. There was close agreement between the genetic and phenotypic correlations coefficients within the F2 generations.

Table 16. Correlation coefficients among Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) using the F2 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

	HEADING DATE			PLANT HEIGHT		
CROSS †	SPC	RCI	SEPFL	SPC	RCI	SEPFL
BOW//K/K	-0.11*	-0.14**	-0.17**	-0.24*	-0.28**	-0.43**
BOW//OAS/TRM	-0.59**	-0.02	-0.42**	-0.37**	-0.19**	-0.52**
BOW/CNO	-0.42**	-0.16**	-0.08**	-0.48**	-0.57**	-0.70**
K/K//OAS/TRM	-0.10**	-0.10*	-0.13*	-0.43**	-0.43**	-0.48**
K/K//CNO	-0.28**	-0.29**	-0.33**	-0.35**	-0.36**	-0.42**
OAS/TRM//CNO	-0.09*	-0.12*	-0.11*	-0.70**	-0.71**	-0.75**

† BOW = Bobwhite "S", OAS/TRM = Oasis/Torim, CNO = Ciano 79, K/K = Kavkaz/K4500 L.A.4

*, **, Significant at the 0.05 and 0.01 probability level

N = Total number of plants in F2, 400.

Table 17. Correlation coefficients among Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) using the F3 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

	HEADING DATE			PLANT HEIGHT		
CROSS †	SPC	RCI	SEPFL	SPC	RCI	SEPFL
BOW//K/K	-0.11*	-0.13*	-0.13*	-0.14*	-0.18**	-0.23**
BOW//OAS/TRM	-0.33**	-0.33**	-0.29**	-0.45**	-0.46**	-0.50**
BOW/CNO	-0.33**	-0.33**	-0.31**	-0.70**	-0.70**	-0.73**
K/K//OAS/TRM	-0.13**	-0.13**	-0.07*	-0.64**	-0.64**	-0.67**
K/K//CNO	-0.65**	-0.65**	-0.62**	-0.62**	-0.61**	-0.63**
OAS/TRM//CNO	-0.56**	-0.55**	-0.52**	-0.75**	-0.74**	-0.77**

† BOW = Bobwhite "S", OAS/TRM = Oasis/Torim, CNO = Ciano 79, K/K = Kavkaz/K4500 L.A.4

*, **, Significant at the 0.05 and 0.01 probability level

N = Total number of plants in F3, 192.

DISCUSSION

Worldwide over 50 million hectares of wheat mainly distributed in the high rainfall areas are vulnerable to Septoria leaf blotch (Sanjaya Rajaram personal communication). It is in these areas that a concerted effort has been made to develop resistant cultivars. This need has led to the identification and incorporation of new sources of resistance in adapted wheat cultivars, and to a better understanding of the pathogen - host relationship. Although monogenic inherited resistance conditioned by dominant, or partially dominant, and recessive genes have been reported in different wheat germplasm (Eyal et al. 1985), the number of genes and nature of the gene action varies depending on the genetic background of the cultivars selected. Parents selected for this study have shown a broad base of resistance to Septoria leaf blotch on a global basis. The question why some cultivars have more durable type of resistance remains to be investigated and was the focus of this investigation. Wheat cultivars reported to be resistant in one environment have not been resistant in other environments (Eyal et al. 1985) this suggests the importance of identifying a more broad type resistance. Thus, it is important to determine how durable genetic resistance can be achieved.

These is also a tendency for short and early maturing wheat cultivars to be more susceptible to S. tritici (Rosielle (1972), Danon et al. (1982), Eyal et al. (1983), and Beuningen and Kohli (1988)). This has limited plant breeders in their selection of certain genotypes. An understanding of the nature of gene action involved in the inheritance of resistance to Septoria leaf blotch and the possible relationship among different traits influencing resistance, would help in developing strategies to incorporate more durable resistance to S. tritici into agronomically acceptable wheat cultivars.

I. Frequency Distribution

In this study the large environmental variation influencing the disease traits and the continuous distribution of the segregating populations made it impossible to classify plants into discrete classes. These results are similar to those reported by Camacho-Casas (1989) who suggested a quantitative mode of inheritance influencing the expression of the disease traits. As a consequence no attempt was made to estimate the number of genes governing Septoria leaf blotch resistance in the experimental material used in this investigation.

Crosses between resistant x susceptible parents showed that the mean values of the three disease traits among the F1, F2, and F3 populations were near the midparent values, except for Septoria flag leaf severity. This indicates that the nature of inheritance of resistance to Septoria leaf blotch was mainly the result of genes functioning in an additive manner.

Transgressive segregation was observed toward susceptibility in F2 and F3 progeny from crosses between resistant parents. This is significant in that the resistant parents appear to have different genetic factors for resistance. It is of interest to note that in this study the presence of several resistance genes found in

Bobwhite "S" and Kavkaz/K4500 L.A.4 are in agreement with those reported by Eyal et al. (1985), for the same lines respectively using a gene-for-gene analysis. With different genetic sources of resistance among these cultivars a more durable type resistance to Septoria leaf blotch may be possible in future cultivars.

II. Nature of Gene Action

Highly significant differences among the F1, F2, and F3 generations indicated the presence of great genotypic variability in these populations for the five traits measured. Significant differences were observed for both GCA and SCA among the F1, F2, and F3 generations. This indicates that the genetic variation among generations was made up of both additive and nonadditive gene action for Septoria progress coefficient, Relative coefficient of infection, Septoria flag leaf severity, Heading date, and Plant height. However, GCA values were always higher and accounted for much of the genetic variation; therefore, additive gene action effects appeared to be most important in the inheritance of the five traits evaluated. This is supported also by the ratios of GCA/SCA which exceeded the SCA. These results are in agreement with those of Van Ginkel and Scharen (1987) and by Danon and Eyal (1989), where it was suggested that additive gene effects were the major component of genetic variation, but the SCA effects were present in all crosses. This would suggest that selection in early generations such as F2 and F3 would be effective due to the largely additive genetic variation associated with these traits. These results are not in agreement with those reported by Camacho-Casa (1989) who observed the presence of a large nonadditive gene action effects for the same traits, leading him to conclude that selection for resistance to S. tritici has to be delayed until high level of homozygosity is obtained.

In estimating the genetic components of variance for the disease traits it was apparent that not all of the disease traits used to estimate the degree of S. tritici infection can be applied effectively in selecting for resistance. Genetic components of variance for Septoria progress coefficient (SPC, proposed by Eyal et al. (1987), showed that genetic variation was nearly equal for σ^2 GCA and σ^2 SCA. This indicates that the genetic variation of the genotypes for this characters were influenced by both additive and nonadditive gene action effects. In this study, GCA/SCA ratios were low, suggesting that nonadditive gene action played an important role in the expression of Septoria leaf blotch. Therefore, selection for resistance using this trait should be delayed until later generations.

When the genetic components for Relative coefficient of infection were evaluated, a higher σ^2 GCA in both F2 and F3 generations were observed. This suggests that genes which behave in an additive manner were more important. However, the GCA/SCA ratios in the F1 and F2 were low, suggesting again for this trait that nonadditive gene action played a significant role. Thus, selection for resistance using this character should be practiced in later generations.

The genetic components for Septoria flag leaf severity (percentage of flag leaf area affected by S. tritici), showed that the estimates of genetic variation were nearly equal for σ^2 GCA and σ^2 SCA in the F2 generation, but the σ^2 GCA was higher in the F3 generation. This indicated that variation of the genotypes was associated in equal importance for both additive and nonadditive effects in the F2 generation, while additive gene action effects were more important in determining the expression of resistance to S. tritici in the F3 generation. Therefore, selection using this criteria should be delayed until the F3 generation.

The relative contribution of the parental genotypes to Septoria leaf blotch resistance was accomplished by comparing the individual estimates of the GCA effects. Negative values indicate a contribution towards resistance while positive values illustrate the opposite. In this study, the parents Bobwhite "S" and Kavkaz/K4500 L.A.4 had the largest negative GCA effects for all disease traits suggesting that Bobwhite "S" and Kavkaz/K4500 L.A.4 would be the best sources for genetic resistance to S. tritici. The parent Oasis/Torim had moderately positive GCA effects for all disease traits. However, since it also carries different genes for resistance it could be a useful parent. However it might be necessary to grow larger F2 populations to ensure that the desired genetic combination were realized.

Generally, the magnitude and sign of the GCA effects of each parent were in agreement with the individual performance in the field.

III. Heritability

To provide additional information regarding the amount of genetic variability for Septoria leaf blotch resistance, narrow-sense heritability estimates were calculated for each of the crosses. As a measure of additive gene action, narrow sense heritability estimates are expected to increase as the generation are advanced. In this study, heritability estimates for all traits obtained through generations showed a consistent tendency to be high in the F1, decrease in the F2, and increase again in the F3 generation. However, the magnitude of these estimates were consistently low for Septoria progress coefficient and Relative coefficient of infection, suggesting that progress to select for resistance should not be effective in early generations specially in the F2 generation for these traits. This is supported also by the low GCA/SCA ratios, and the low genetic components obtained for Septoria progress coefficient in the F2 and F3, and the lack of agreement between the additive effects found in the gene action analysis and the nonadditive effects observed in the heritability estimates for Relative coefficient of infection in the F2 generation. Therefore, due to the inconsistency of the data, selection using these disease traits may not be effective.

This was not the case for the Septoria flag leaf severity trait which showed the highest heritability estimates observed through generations among the disease traits. Of the disease traits substantial breeding progress could be made using this character as a measured to select for resistance, especially in the F3 where heritability estimates were markedly higher when compared to the rest of the traits. This observation is in agreement with those reported by Rajaram (1989), in which the CIMMYT's breeding criteria recognizes the effects of resistance via slower pathogen growth on the flag leaf.

Heritability estimates for the five traits in the F3 generation were high. These estimates suggest that progress in selecting for resistance to S. tritici should be possible as a large part of the genetic variation is additive. Thus, plant breeders can effectively select for resistance within and between crosses, and eliminate the less productive crosses from the segregating populations.

The narrow-sense heritability estimates for the disease traits, and involving the six crosses were higher for Septoria flag leaf severity than for Septoria progress coefficient and Relative coefficient of infection. The largest narrow-sense heritability among crosses was obtained in Oasis/Torim//Ciano 79, followed by Kavkaz/K4500 L.A.4//Oasis/Torim and Kavkaz/K4500 L.A.4//Ciano 79. From these results it may be concluded that in these particular crosses, breeding progress for resistance to S. tritici would be effective in the F3 generation using the Septoria flag leaf severity character as a selection criteria.

IV. Phenotypic and Genetic Correlations

Concern has often been expressed that semidwarf early maturing cultivars of wheat tend to be more susceptible to Septoria leaf blotch than tall late maturing cultivars (Rosielle 1972, Eyal et al 1983, and Beuningen and Kohli 1988). The significant negative correlations observed among the F2 and F3 populations between the disease traits related to S. tritici and heading date and plant height, support this popular belief previous noted.

Despite the significant variation in the disease traits, there was a moderate negative phenotipic and genetic correlations between amount of disease and plant height in the F2 and F3 generation. This indicated that resistance and height did not segregate independently. Studies concerning these traits show a clear tendency for them to be associated together and either genetic linkage or pleiotropy have been suggested (Shaner et al. 1975, Baltazar, 1987).

However, the consistent moderate and low associations in some crosses indicate that short early maturing resistant plants can be found. In this study, the recovery of such types of plants confirm that semidwarf plants have good S. tritici resistance. This suggests genetic linkage rather than pleiotropy. Similar results have been obtained by other researchers (Rosielle and Brown, 1979, Danon et al., 1982)

BREEDING STRATEGY

Genetic variability was found among the resistant parents used in this investigation. Resistance to Septoria leaf blotch observed in Bobwhite "S", Kavkaz/K4500 L.A.4 and Oasis/Torim appeared to be quantitatively inherited based on the continuous distribution observed in the F2 and F3 generation. Also transgressive segregation toward resistance and susceptibility was observed in all crosses between resistant x resistant parent. It shows that the parents carry different genes for resistance. Since both combining ability and narrow-sense heritability estimates suggested additive gene effects to be the major component of the genetic variation, selection in early generations would be effective. Septoria flag leaf severity trait showed the highest heritability estimates of the disease traits. Moderate and low negative phenotypic and genetic correlations were obtained among the F2 and F3 generations for the three disease traits with heading date and plant height.

Results from this investigation, suggests that breeding for Septoria leaf blotch resistance would be effective and that a more durable type of resistance can be achieved. The presence of several different resistance genes in the parents would allow breeders to pyramid more genes through breeding to produce even greater durable resistance to Septoria leaf blotch.

The high GCA and narrow-sense heritability estimates found in the F3 generation provide evidence that substantial progress for resistance to Septoria leaf blotch would be effective selecting in this generation. Also for the three disease traits measured it would appear that selection for the lowest percentage of Septoria infection on the flag leaf would result in the most progress in developing resistant lines.

Furthermore based on the associations between traits it would be possible to obtain early maturing, short stature genotypes from the genetic materials used in this study. However, to obtain such progeny it will be necessary to increase the size of the segregating populations.

SUMMARY AND CONCLUSIONS

The objectives of this investigation were: 1) to determine the mode of inheritance of resistance to Septoria tritici in selected germplasm expressing more durable levels of resistance and 2) to examine the relationships between plant height, heading date and severity of Septoria leaf blotch infection.

Three resistant spring wheat lines and one cultivar susceptible to Septoria leaf blotch were used to developed a 4x4 diallel cross. Parents, F1, F2, and F3 populations were inoculated with one pathogenic strain of Septoria tritici and evaluated under field conditions at CODAGEM, Toluca, Mexico during 1989 crop cycle.

Data were collected on an individual plant basis for heading date, plant height, Septoria progress coefficient, relative coefficient of infection, and percent of Septoria infection on the flag leaf. An analysis of variance for a complete randomized design among the parents, F1, and F2 populations was used to test the hypothesis that there were no genotypic differences. For the parents and F3 lines a randomized block analysis was employed. Means values for parents and each generation were computed using Tukey studentized range test. Frequency distributions were observed to determine the mode of inheritance. Combining ability analysis were performed using Griffing's (1956) model 1, method 4 and narrow-sense heritability was used to estimate the nature of the gene action. Phenotypic correlations were calculated to examine the possible associations between the disease traits and their relationships with heading date and plant height.

Based on the results of this study the following conclusions were made:

1. Differences were obtained between parents and among F1, F2, and F3 generations for all traits, except plant height for the two shortest parents.
2. Frequency distributions were continuous for the disease traits in all populations among crosses in the F2 and F3 generation, suggesting a quantitative mode of inheritance.
3. Transgressive segregation toward susceptibility was evident in all progeny of resistant x resistant crosses, indicating that the parents have different genes for resistance to Septoria leaf blotch.
4. Combining ability analysis indicated that additive genes effects were the major component of genetic variation; however, nonadditive gene action was present in all crosses. Selection in early generations for Septoria leaf blotch resistance would be effective due to the largely additive nature of the gene expression for the three disease traits evaluated.
5. Based on the GCA effects, the resistant Bobwhite "S" and Kavkaz/K4500 L.A.4 were found to be the best parental sources for resistance to Septoria leaf blotch. The parent Oasis/Torim contributed less to the level of resistance.

6. High GCA and narrow-sense heritability estimates in the F3 generation suggest that substantial progress for resistance to Septoria leaf blotch could be made in this generation.

7. The Septoria flag leaf severity trait had the highest narrow-sense heritability estimates of the disease traits measured. Making it the most promising when selecting for disease resistance.

8. A high positive association was found among the disease traits evaluated. Moderate and low negative phenotypic and genetic correlations were obtained among the F2 and F3 populations between the disease traits with heading date and plant height. This indicates that the selection of early maturing, short statured plants would be possible within the populations employed in this study.

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APPENDIX

Appendix Table 1. Means, standard deviation and midparent values for Septoria progress coefficient (SPC) observed in F1 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	MIDPARENT
Bobwhite "S"//Kavkaz/K4500 L.A.4	0.52±0.09 ab †	0.34
Bobwhite "S"//Oasis/Torim	0.65±0.11 d	0.50
Bobwhite "S"/Ciano 79	0.55±0.15 abc	0.60
Kavkaz/K4500 L.A.4//Oasis/Torim	0.59±0.10 bcd	0.56
Kavkaz/K4500 L.A.4//Ciano 79	0.50±0.07 a	0.65
Oasis/Torim//Ciano 79	0.62±0.04 cd	0.81

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 2. Means, standard deviation and midparent values for Relative coefficient of infection (RCI) observed in F1 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	MIDPARENT
Bobwhite "S"//Kavkaz/K4500 L.A.4	34.37± 7.73 a †	22.48
Bobwhite "S"//Oasis/Torim	50.47± 8.15 c	33.84
Bobwhite "S"/Ciano 79	38.72±10.19 ab	44.17
Kavkaz/K4500 L.A.4//Oasis/Torim	41.14±6.73 b	39.05
Kavkaz/K4500 L.A.4//Ciano 79	38.02±5.59 ab	49.37
Oasis/Torim//Ciano 79	43.56±3.04 b	60.74

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 3. Means, standard deviation and midparent values for Septoria flag leaf (SEPFL) observed in F1 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	MIDPARENT
Bobwhite "S"//Kavkaz/K4500 L.A.4	18.4±13.1 a †	11.7
Bobwhite "S"//Oasis/Torim	58.0±10.0 c	30.3
Bobwhite "S"/Ciano 79	31.2±13.9 b	45.7
Kavkaz/K4500 L.A.4//Oasis/Torim	54.0±17.5 c	39.6
Kavkaz/K4500 L.A.4//Ciano 79	35.2± 5.1 b	54.9
Oasis/Torim//Ciano 79	49.6±11.0 c	73.5

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 4. Means, standard deviation and midparent values for Heading date (HD) observed in F1 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	MIDPARENT
Bobwhite "S"//Kavkaz/K4500 L.A.4	82.84±0.37 b †	83.7
Bobwhite "S"//Oasis/Torim	84.28±0.46 c	87.1
Bobwhite "S"/Ciano 79	79.80±0.41 a	77.6
Kavkaz/K4500 L.A.4//Oasis/Torim	86.08±0.28 d	89.6
Kavkaz/K4500 L.A.4//Ciano 79	84.24±0.44 c	80.1
Oasis/Torim//Ciano 79	86.16±0.37 d	83.5

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 5. Means, standard deviation and midparent values for Plant Height (PHGT) observed in F1 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	MIDPARENT
Bobwhite "S"//Kavkaz/K4500 L.A.4	95.2±0.58 c †	87.5
Bobwhite "S"//Oasis/Torim	89.3±0.85 b	83.9
Bobwhite "S"/Ciano 79	80.4±0.70 a	80.1
Kavkaz/K4500 L.A.4//Oasis/Torim	104.4±1.66 d	91.4
Kavkaz/K4500 L.A.4//Ciano 79	96.5±0.51 d	87.5
Oasis/Torim//Ciano 79	89.6±0.76 b	84.0

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 6. Means, standard deviation and Range for Septoria progress coefficient (SPC) observed in F2 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	RANGE
Bobwhite "S"//Kavkaz/K4500 L.A.4	0.47±0.12 a †	0.11 - 0.89
Bobwhite "S"//Oasis/Torim	0.74±0.16 d	0.24 - 1.10
Bobwhite "S"/Ciano 79	0.52±0.18 b	0.11 - 1.02
Kavkaz/K4500 L.A.4//Oasis/Torim	0.78±0.21 e	0.25 - 1.13
Kavkaz/K4500 L.A.4//Ciano 79	0.64±0.23 c	0.25 - 1.12
Oasis/Torim//Ciano 79	0.67±0.20 c	0.12 - 1.04

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 7. Means, standard deviation and Range for Relative coefficient of infection (RCI) observed in F2 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	RANGE
Bobwhite "S"//Kavkaz/K4500 L.A.4	35.79±10.81 a †	4.93 - 60.49
Bobwhite "S"//Oasis/Torim	51.81±11.65 de	12.34 - 77.78
Bobwhite "S"/Ciano 79	38.87±14.78 b	2.47 - 77.78
Kavkaz/K4500 L.A.4//Oasis/Torim	54.06±14.66 e	7.41 - 77.78
Kavkaz/K4500 L.A.4//Ciano 79	43.56±16.86 c	12.35 - 77.78
Oasis/Torim//Ciano 79	49.32±15.89 d	8.64 - 77.78

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 8. Means, standard deviation and Range for Septoria flag leaf (SEPFL) observed in F2 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	RANGE
Bobwhite "S"//Kavkaz/K4500 L.A.4	25.5±18.0 a †	00.0 - 70.0
Bobwhite "S"//Oasis/Torim	51.7±20.4 c	00.0 - 90.0
Bobwhite "S"/Ciano 79	29.5±22.7 b	00.0 - 90.0
Kavkaz/K4500 L.A.4//Oasis/Torim	56.0±25.4 c	00.0 - 90.0
Kavkaz/K4500 L.A.4//Ciano 79	36.0±26.7 b	00.0 - 90.0
Oasis/Torim//Ciano 79	41.2±27.4 c	00.0 - 90.0

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 14. Means, standard deviation and Range for Heading date (HD) observed in F2 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	RANGE
Bobwhite "S"//Kavkaz/K4500 L.A.4	83.29±5.68 bc †	67.0 - 104.0
Bobwhite "S"//Oasis/Torim	85.76±4.85 e	73.0 - 98.0
Bobwhite "S"/Ciano 79	82.56±4.56 b	70.0 - 104.0
Kavkaz/K4500 L.A.4//Oasis/Torim	83.82±3.94 cd	69.0 - 98.0
Kavkaz/K4500 L.A.4//Ciano 79	78.80±6.99 a	66.0 - 108.0
Oasis/Torim//Ciano 79	84.85±5.74 de	68.0 - 112.0

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 10. Means, standard deviation and Range for Plant Height (PHGT) observed in F2 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	RANGE (cm)
Bobwhite "S"//Kavkaz/K4500 L.A.4	84.0±11.19 b †	55.0 - 115.0
Bobwhite "S"//Oasis/Torim	77.2± 7.27 a	50.0 - 110.0
Bobwhite "S"/Ciano 79	81.9±15.33 b	45.0 - 120.0
Kavkaz/K4500 L.A.4//Oasis/Torim	93.3±13.33 d	60.0 - 135.0
Kavkaz/K4500 L.A.4//Ciano 79	92.9±12.78 d	55.0 - 130.0
Oasis/Torim//Ciano 79	88.63±18.18 c	45.0 - 140.0

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 11. Means, standard deviation and Range for Septoria progress coefficient (SPC) observed in F3 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	RANGE
Bobwhite "S"//Kavkaz/K4500 L.A.4	0.39±0.13 a †	0.22 - 0.90
Bobwhite "S"//Oasis/Torim	0.60±0.18 bc	0.24 - 1.10
Bobwhite "S"/Ciano 79	0.59±0.21 b	0.22 - 0.99
Kavkaz/K4500 L.A.4//Oasis/Torim	0.57±0.19 b	0.23 - 1.05
Kavkaz/K4500 L.A.4//Ciano 79	0.59±0.18 b	0.21 - 1.00
Oasis/Torim//Ciano 79	0.65±0.19 c	0.20 - 1.00

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 12. Means, standard deviation and Range for Relative coefficient of infection (RCI) observed in F3 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	RANGE
Bobwhite "S"//Kavkaz/K4500 L.A.4	28.10±11.18 a †	9.88 - 69.14
Bobwhite "S"//Oasis/Torim	42.83±12.54 b	14.81 - 77.78
Bobwhite "S"/Ciano 79	44.78±16.49 b	14.81 - 77.78
Kavkaz/K4500 L.A.4//Oasis/Torim	41.89±14.67 b	12.35 - 77.78
Kavkaz/K4500 L.A.4//Ciano 79	48.49±15.41 c	12.35 - 77.78
Oasis/Torim//Ciano 79	54.69±15.49 d	9.87 - 77.78

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 13. Means, standard deviation and Range for Septoria flag leaf (SEPFL) observed in F3 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	RANGE
Bobwhite "S"//Kavkaz/K4500 L.A.4	17.9±17.4 a †	00.0 - 80.0
Bobwhite "S"//Oasis/Torim	44.5±22.8 bc	00.0 - 90.0
Bobwhite "S"/Ciano 79	43.9±26.0 bc	00.0 - 90.0
Kavkaz/K4500 L.A.4//Oasis/Torim	39.8±24.4 b	00.0 - 90.0
Kavkaz/K4500 L.A.4//Ciano 79	48.7±25.1 c	00.0 - 90.0
Oasis/Torim//Ciano 79	60.5±25.1 d	00.0 - 90.0

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 14. Means, standard deviation and Range for Heading date (HD) observed in F3 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	RANGE
Bobwhite "S"//Kavkaz/K4500 L.A.4	85.55±3.55 d †	75.0 - 92.0
Bobwhite "S"//Oasis/Torim	86.61±2.21 e	79.0 - 91.0
Bobwhite "S"/Ciano 79	81.15±3.70 b	72.0 - 89.0
Kavkaz/K4500 L.A.4//Oasis/Torim	86.25±2.18 e	81.0 - 93.0
Kavkaz/K4500 L.A.4//Ciano 79	80.35±5.74 a	69.0 - 90.0
Oasis/Torim//Ciano 79	84.09±3.51 c	75.0 - 93.0

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 15. Means, standard deviation and Range for Plant Height (PHGT) observed in F3 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

CROSS	MEAN and ST DEV	RANGE (cm)
Bobwhite "S"//Kavkaz/K4500 L.A.4	89.6±10.48 b †	63.0 - 118.0
Bobwhite "S"//Oasis/Torim	82.6± 6.16 a	67.0 - 102.0
Bobwhite "S"/Ciano 79	83.4±12.87 a	53.0 - 114.0
Kavkaz/K4500 L.A.4//Oasis/Torim	92.9±11.29 c	65.0 - 123.0
Kavkaz/K4500 L.A.4//Ciano 79	91.8± 9.97 bc	70.0 - 114.0
Oasis/Torim//Ciano 79	90.9±16.15 bc	55.0 - 138.0

† Tukey studentized range test; means in the column having at least one letter in common are not significantly different at the 0.05 probability level.

Appendix Table 16. Frequencies of Septoria progress coefficient (SPC) in crosses between resistant x susceptible involving parents, F1, F2, and F3 generation grown at CODAGEM, Toluca, Mexico, 1989.

	Resist.	Intermediate			Suscept.			
Parent and Cross†	10-25	30-45	50-60	65-75	80-95	100>	Total	Mean
BOW "S" --- CNO 79	32	16	2		37	13	50	0.60*
F1	3	1	15	6			25	0.55
F2	36	163	89	65	44	3	400	0.52
F3	4	18	18	5	17	2	64	0.59
K/K --- CNO 79	4	19	27		37	13	50	0.65*
F1		13	12				25	0.50
F2	21	66	156	62	49	46	400	0.64
F3	8	4	33	7	9	3	64	0.59
OAS/TRM --- CNO 79			11	31	8-37	13	50	0.81*
F1			23	2			25	0.62
F2	6	31	139	87	111	26	400	0.67
F3	1	3	9	5	23	23	64	0.65

† BOW "S" = Bobwhite "S", K/K = Kavkaz/K4500 L.A.4 , OAS/TRM = Oasis/Torim, CNO 79 = Ciano 79.

* Midparent value.

Appendix Table 17. Frequencies of Relative coefficient of infection (RCI) in crosses between resistant x susceptible involving parents, F1, F2, and F3 generation grown at CODAGEM, Toluca, Mexico, 1989.

	Resist.	Intermediate			Suscept.			
Parent and Cross†	<5-15	20-30	35-45	50-60	65-75	80>	Total	Mean
BOW "S" --- CNO 79	25	23	2		37	13	50	44.17*
F1		4	8	13			25	38.72
F2	24	89	174	95	15	3	400	38.87
F3	3	11	8	23	7	12	64	44.78
K/K --- CNO 79	2	27	19	2	37	13	50	49.37*
F1		2	11	12			25	38.02
F2	17	76	150	111	21	25	400	43.56
F3	1	7	4	33	7	12	64	48.49
OAS/TRM --- CNO 79			3	39	8	50	50	60.74*
F1			1	24			25	43.56
F2	6	42	129	150	47	26	400	49.32
F3	1		10	19	12	22	64	54.69

† BOW"S" = Bobwhite "S", K/K = Kavkaz/K4500 L.A.4 , OAS/TRM = Oasis/Torim, CNO 79 = Ciano 79.

* Midparent value.

Appendix Table 18. Frequencies of Septoria Percent on flag leaf (SEPFL) in crosses between resistant x susceptible involving parents, F1, F2, and F3 generation grown at CODAGEM, Toluca, Mexico, 1989.

	Resist.	Intermediate			Suscept.		
Parent and Cross†	0-10	20-30	40-50	60-70	80-90	Total	Mean
BOW "S" --- CNO 79	40	1			50	50	45.7*
F1	2	12	11			25	31.2
F2	132	109	102	42	15	400	29.5
F3	9	11	19	10	15	64	43.9
K/K --- CNO 79	21	23	6		50	50	54.9*
F1		25				25	35.2
F2	112	83	115	45	45	400	36.0
F3	4	7	26	12	15	64	48.7
OAS/TRM --- CNO 79		2	15	30	3-50	50	73.5*
F1		3	13	9		25	49.6
F2	88	82	96	85	49	400	41.2
F3	1	6	16	12	29	64	60.5

† BOW "S" = Bobwhite "S", K/K = Kavkaz/K4500 L.A.4 , OAS/TRM = Oasis/Torim, CNO 79 = Ciano 79.

* Midparent value.

Appendix Table 19. Frequencies of Septoria progress coefficient (SPC) in crosses between resistant x resistant involving parents, F1, F2, and F3 generation grown at CODAGEM, Toluca, Mexico, 1989.

	Resist.	Intermediate			Suscept.			
Parent and Cross†	10-25	30-45	50-60	65-75	80-95	100>	Total	Mean
BOW "S" --- K/K	32-4	16-19	2-27				50	0.34*
F1		4	20	1			25	0.52
F2	21	201	122	54	1		400	0.47
F3	18	21	23	1	1		64	0.39
BOW "S"---OAS/TRM	32-0	16-0	2-11	0-31	0-8		50	0.50*
F1		3	4	12	6		25	0.65
F2	1	6	119	146	85	43	400	0.74
F3	2	8	9	33	9	3	64	0.60
K/K --- OAS/TRM	4-0	19-0	27-11	0-31	0-8		50	0.56*
F1			22	2	1		25	0.59
F2	3	11	119	108	57	102	400	0.78
F3	4	11	26	9	12	2	64	0.57

† BOW"S" = Bobwhite "S", K/K = Kavkaz/K4500 L.A.4 , OAS/TRM = Oasis/Torim,
* Midparent value.

Appendix Table 20. Frequencies of Relative coefficient of infection (RCI) in crosses between resistant x resistant involving parents, F1, F2, and F3 generation grown at CODAGEM, Toluca, Mexico, 1989.

	Resist.	Intermediate			Suscept.			
Parent and Cross†	<5-15	20-30	35-45	50-60	65-75	80>	Total	Mean
BOW "S"--- K/K	25-2	23-27	2-19	0-2			50	22.48*
F1		24	1				25	34.37
F2	20	89	235	56			400	35.79
F3	12	27	23		2		64	28.10
BOW "S"-- OAS/TRM	25-0	23-0	2-3	0-39	0-8		50	33.84*
F1			7	12	6		25	50.47
F2	2	11	112	232		43	400	51.81
F3		10	34	8	11	1	64	42.83
K/K --- OAS/TRM	2-0	27-0	19-3	2-39	0-8		50	39.05*
F1			22	2	1		25	41.14
F2	2	15	116	165	48	54	400	54.06
F3	1	14	26	14	8	1	64	41.89

† BOW "S" = Bobwhite "S", K/K = Kavkaz/K4500 L.A.4 , OAS/TRM = Oasis/Torim,
* Midparent value.

Appendix Table 21. Frequencies of Septoria Percent on flag leaf (SEPFL) in crosses between resistant x resistant involving parents, F1, F2, and F3 generation grown at CODAGEM, Toluca, Mexico, 1989.

	Resist.		Intermediate		Suscept.		
Parent and Cross†	0-10	20-30	40-50	60-70	80-90	Total	Mean
BOW "S"--- K/K	40-21	1-23	0-6			50	11.7*
F1	10	12	3			25	18.4
F2	125	148	101	26		400	25.5
F3	29	19	12	3	1	64	17.9
BOW "S"--- OAS/TRM	40-0	1-2	0-15	0-30	0-3	50	30.3*
F1			10	14	1	25	58.0
F2	16	66	133	139	46	400	51.7
F3	4	7	26	12	15	64	44.5
K/K --- OAS/TRM	21-0	23-2	6-15	0-30	0-3	50	39.6*
F1		4	11	6	4	25	54.0
F2	28	51	108	99	114	400	56.0
F3	10	9	22	14	9	64	39.8

† BOW "S" = Bobwhite "S", K/K = Kavkaz/K4500 L.A.4 , OAS/TRM = Oasis/Torim,
* Midparent value.

Appendix Table 22. Genetic correlation coefficients among Septoria progress coefficient (SPC), Relative coefficient of infection (RCI), Septoria flag leaf severity (SEPFL), Heading date (HD), and Plant height (PHGT) using the F2 generation from a 4x4 diallel cross grown at CODAGEM, Toluca, Mexico, 1989.

	HEADING DATE			PLANT HEIGHT		
CROSS †	SPC	RCI	SEPFL	SPC	RCI	SEPFL
BOW//K/K	-0.18	-0.21	-0.25	-0.37	-0.42	-0.65
BOW//OAS/TRM	-0.59	-0.02	-0.47	-0.36	-0.26	-0.59
BOW/CNO	-0.14	-0.11	-0.02	-1.04	-0.85	-0.88
K/K//OAS/TRM	-0.11	-0.11	-0.18	-0.50	-0.50	-0.69
K/K//CNO	-0.30	-0.31	-0.33	-0.38	-0.40	-0.43
OAS/TRM//CNO	-0.10	-0.12	-0.11	-0.71	-0.73	-0.82

† BOW = Bobwhite "S", OAS/TRM = Oasis/Torim, CNO = Ciano 79,
K/K = Kavkaz/K4500 L.A.4
N = Total number of plants in F2, 400.