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Four isogenic lines possessing different combinations of height reducing genes Rht_1 and Rht_2 from 'Norin 10' were crossed to a short stature, early maturing, septoria susceptible cultivar identified as the 'Tibet Dwarf'. The isogenic lines originated from the backcross population of 'Itana'/3/'Norin 10'/'Brevor 14'//6*'Itana'. Parents, F_1 and F_2 generations provided the experimental materials upon which observations were made.

Differences in reaction to septoria tritici blotch were observed with a specific height reducing gene. When the gene Rht_2 was present either as a isoline or in the progeny a higher degree of resistance was found. The most susceptible disease reaction was measured in the presence of Rht_1 gene.

Associations, as determined by phenotypic and genetic correlations were detected between septoria tritici blotch resistance and tall

stature, late heading and maturity dates. Short stature, early heading and maturing plants with acceptable levels of resistance were identified in the F_2 population when Rht_2 was present.

Either due to some biological limitation or perhaps genetic linkages it will be necessary for wheat breeders to select the appropriate dwarfing source and to grow large F_2 populations to insure obtaining the desired genotypes.

POSSIBLE ASSOCIATION BETWEEN DWARFING GENES Rht_1 AND Rht_2 AND THE REACTION TO SEPTORIA TRITICI BLOTCH IN WINTER WHEAT (*Triticum aestivum* L. em Thell)

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TABLE OF CONTENTS

LIST OF TABLES

List of Tables--------continued

List of Tables--------continued

LIST OF APPENDIX FIGURES

LIST OF APPENDIX TABLES

POSSIBLE ASSOCIATION BETWEEN DWARFING GENES Rht1 AND Rht2 AND THE REACTION TO SEPTORIA TRITICI BLOTCH IN WINTER WHEAT (*Triticum aestivum* L. em Thell)

INTRODUCTION

Septoria tritici is a major foliar pathogen of wheat in many parts of the world. Increased incidence of the leaf blotch disease caused by *S. tritici* is thought by some to be due to the result of the widespread replacement of tall, local cultivars, by the high yielding, early maturing, semidwarf stature wheats.

Many of these semidwarf cultivars possessed one or both of the Norin 10 height reducing genes (Rht_1 or Rht_2) in their parentage. A suggestion has been made that short strawed wheat cultivars are more susceptible to leaf blotch as there is a shorter distances between consecutive leaves "The ladder effect" (Eyal et al. 1981). However, experimental results have been inconsistent when comparisons have been made between plant height, and susceptibility.

Genetic associations between short stature and susceptibility to *S. tritici* have also been suggested. Pleiotropy or linkages between genes that determine plant height and susceptibility to *S. tritici* may explain such an association. However, low correlation values between plant height and severity of the disease have been observed which do not support the hypothesis for pleiotropy between short stature and susceptibility in wheat.

Early maturity is also frequently associated with susceptibility to *S. tritici*. This association may have both genetic and epidemiological considerations. In regions where septoria tritici blotch is a major problem, favorable cold temperatures and rain are more probable early in the life cycle of the plant. Thus, early maturing cultivars are more likely to encounter favorable weather for infection by the pathogen. Genetic linkages between earliness and susceptibility to S. tritici have also been mentioned as a possibility to explain this association.

The tendency of short stature, early maturing cultivars to be more susceptible to S. tritici than the taller, late maturing cultivars would be a constraint to the plant breeder in developing superior wheat cultivars as the amount of genetic variability available would be limited.

This study was conducted to examine the following parameters involving septoria tritici blotch: a) possible association between Rht_1 or Rht_2 and susceptibility, and b) apparent associations among plant height, heading and maturity date and susceptibility.

LITERATURE REVIEW

HISTORICAL ASPECTS OF NORIN 10 DWARFING GENES

The development of short stature wheats was a major accomplishment of 20th century agriculture. Semidwarf genes most extensively used were Rht_1 and Rht_2. These so-called 'Daruma' genes were found in the Japanese cultivar 'Norin 10' (Kulshrestha 1978 et al.). According to Gale et al. (1981), the 'Norin 10' cultivar was first introduced into the United States in 1946 by S. C. Salmon. Their value as a genetic source of short stiff straw, was first recognized and used by O. E. Vogel at Washington State University in 1949. His objective was to develop short, stiff straw cultivars which could resist lodging in eastern Washington where nitrogen tended to accumulate at the bottom of the hill sides.

The use of the Norin 10 genes by N. E. Borlaug in the Rockefeller Foundation wheat program located in Mexico increased the impact that these genes had on world wheat production. Higher yields obtained with the new short stature cultivars in India, Pakistan, Mexico and many other third world countries coupled with Borlaug's ability to convince national governments to provide the necessary inputs, i.e. fertilizers, led to his receiving the Nobel Peace Prize in 1970.

From 1970 to date, several reports have been published to elucidate the influence of Norin 10 genes on yield and other agronomic traits. Selections with the dwarfing gene Rht_1 have shown advantages over those with Rht_2 for grain yield, test weight, 1000 kernel weight, emergence rate index, and a longer coleoptile. Selections with Rht_1 also appear better adapted to unfavorable growing conditions than cultivars with the Rht_2 (Allan 1970).

Grain number per spike, grain size and tiller number have been mentioned by Gale et al. (1985) to be affected by the use of either Rht_1 or Rht_2. They reported that the trend is for increased grain number to be associated with, but not entirely compensated by, decreased grain size. In their investigation spikelet number per spike was not affected and thus the increase in grain number reflects increased spikelet fertility.

Allan (1983) reported that mean yields of lines with either Rht_1 or Rht_2 genes were generally superior to those with the both dwarf genes Rht_1Rht_2. This result may explain the near universal use of the one dwarf gene rather than two to reduce plant height and enhance yield.

ASSOCIATION OF DWARFING GENES AND Septoria spp.

Most reports concerning the Norin 10 genes have shown the beneficial effects of these genes on yield. However, other studies have suggested the association of these genes with other less desireable factors such as susceptibility to specific diseases.

Studies which provide information about the association of the Rht genes, and possible linkages, are generally of two types (Gale et al. 1985). They either compare groups of "random lines" which differ in their Rht allele derived by selfing single cross hybrids, or employ "isogenic lines" in which different alleles have been isolated in a specified genetic background.

Scott et al. (1982) observed that among F_3 and F_4 randomly selected families, there was a clear tendency for tall stature and resistance to S. nodorum to segregate together. They suggested that the association between these characters was not fortuitous and provided evidence of linkage or pleiotropy. There was a similar, though less consistent tendency for late spike emergence and resistance to be associated. They proposed that resistance is under pleiotropic control rather than linkage.

A further study was conducted by Scott et al. (1985) to determine the effect of S. nodorum on plant height. F_3 randomly selected families from a cross between tall and dwarf cultivars possessing the Rht_2 dwarfing gene were included. They observed that despite the large effects of the Rht_2 gene on height, there was not a corresponding reaction to S. nodorum. However, plants with Rht_2 tended to be more resistant to S. nodorum than other height levels. It was concluded that Rht_2 enables breeders to select for shorter stature without increasing the level of susceptibility to S. nodorum.

It has been suggested that the appearance of S. tritici in the Mediterranean region resulted from the introduction of semidwarf wheats. However, Rajaram et al. (1977) noted that S. tritici was reported 30-40 years ago, and severe infections were observed during the 1950's in Tunisia. While the land race cultivars of the Mediterranean region appear to have adequate levels of resistance when grown under traditional conditions, these same cultivars become highly susceptible if grown under higher fertility levels and in denser plant populations.

As noted by Saari et al. (1974) the semidwarf wheats were not responsible for introducing the Septoria problem to the Mediterranean region but have focused attention on it.

Using different sources of resistance to S. tritici, a considerable number of semidwarf, high-yielding lines resistant to S. tritici have been selected by breeders from the International Maize and Wheat Improvement Center (CIMMYT), spring wheat breeding program. This suggests that the semidwarf character is not closely linked to susceptibility to S. tritici (Mann et al. 1985).

According to Eyal et al. (1987) previous studies have shown that the dwarfing gene Rht_2 has only a slight effect on resistance to S. tritici. Therefore, the relationship between height and resistance appears to be determined by genes other than Rht_2.

Conversely, Scott et al. (1985) reported that taller cultivars of wheat tended to be more resistant than dwarf cultivars to both S. nodorum and S. tritici. However, they suggested that this might not indicate a genetic relationship between height and resistance, but merely reflect a fortuitous susceptibility in the Japanese donors of dwarfing genes.

Four mechanisms that might be responsible for the association between short stature wheats and susceptibility to S. nodorum have been suggested by Scott et al (1982). These include: a) dispersal of S. nodorum from the base to the top of the plant occurs more readily when the distance to be traveled by the pycnidiospores is less, b) canopy of the shorter cultivars might generate a microclimate that is more conducive to the development of S. nodorum, c) shorter cultivars may often be earlier maturing and therefore more susceptible at a given time, and d) short stature, and early maturity cultivars might be genetically associated with susceptibility to S. nodorum. Thus, suggesting a tendency for short stature, early maturity, and susceptibility to segregate together.

Results of three field experiments conducted by Scott et al. (1985) were consistent with the hypothesis that the canopies of taller wheat cultivars generate a less favorable microclimate for development of S. nodorum. They observed: a) measurements of photosynthetic area per unit volume of space occupied by canopies showed that taller cultivars had lower canopy densities than shorter cultivars, b) less disease development in artificially thinned canopies of taller rather than shorter cultivars, and c) less disease development in plots raised on mounds compared to plots sunk in trenches. Nevertheless, they concluded that a microclimatic effect is only one of several mechanisms that contribute to the tendency for taller cultivars to be more resistant.

According to Eyal et al. (1981) the vertical progress of S. tritici from the lower to upper part of the plant is affected by the distances between consecutive leaves, "The ladder effect". They suggested that in dwarf cultivars the chances of pycnidiospores reaching the upper plant parts responsible for grain filling is greater than in taller cultivars. However, in severe Septoria epidemics they concluded that these differences are readily overcome.

Eyal et al. (1982) reported that the progress of epidemics caused by S. tritici in the dwarf cultivar 'Bet-Dagan 213' proceeded faster than that of the taller semidwarf cultivar 'Lakhish 221'. On 'Lakhish 221', the disease did not reach the upper plant leaves and spike as in the case of the dwarf cultivar. The regression coefficient for the ratio between disease progression to plant development for tall cultivars was b=0.8043, in contrast to b=1.1677 observed with dwarf cultivars.

In other studies carried out to demonstrate the association between plant height and susceptibility to Septoria diseases, a negative association between these traits has been reported.

Scott et al. (1985) reported that among F_3 randomly selected families resulting from a cross between tall resistant and dwarf susceptible cultivars, plant height was negatively correlated with the incidence of both S. nodorum and S. tritici. They concluded that this was not the result of a common relationship with height, as no significant correlation existed with resistance to S. tritici.

Small negative correlations were reported between plant height and S. tritici pycnidial coverage in F_1 and F_2 populations derived from crosses between tall, resistant, late maturing and short, susceptible, and early maturing cultivars (Danon et al. 1982). They reported that this low correlation did not support the hypothesis of linkage or pleiotropy between short-stature wheats and susceptibility. However, short stature (50-60 cm), resistant plants were recovered in F_2 populations which continue to express their resistance in succeeding generations.

In a similar study carried out to determine the association between S. tritici and plant height, Danon et al. (1986) reported low correlations between these two traits among F_1, F_2, F_3 and backcross populations derived from crosses among spring and winter habit wheat cultivars.

ASSOCIATION BETWEEN MATURITY DATE AND RESISTANCE TO S.tritici

Resistance to septoria tritici blotch in wheat has also been found to be negatively associated with late heading and physiological maturity. This association may have both genetic and epidemiological considerations (Eyal et al. 1981).

Based on simple correlations (r) and determination coefficients (r^2) Tavella (1978) observed that the taller and later maturing the cultivar the lower its septoria tritici blotch score. He concluded that plant height explained 61% of the variation in disease incidence, with 44% due to date of heading. In a second experiment, date of heading explained 72% and plant height 45% of the variation associated with the disease incidence.

According to Rosielle et al. (1979) genotypic correlations of S. tritici infection scores with heading and late maturity were negative in F_2 and F_3 generations derived from crosses between resistant spring cultivars 'Seabreeze', 'Veranopolis', and 'IAS-20' and the susceptible cultivar 'Gamenya'. The largest correlation values (r=-0.53) occurred in 'Gamenya x IAS-20' for heading and for plant height (r=-0.57) in 'Gamenya' x 'Seabreeze'.

Among parental F_1, F_2, F_3 and backcross populations derived from crosses among spring and winter cultivars in a complete diallel scheme, Danon et al. (1986) reported low correlations between heading date, and pycnidial coverage.

Danon et al. (1982) reported moderate negative correlations between susceptibility to *S. tritici* and heading date among crosses between tall, resistant, late maturing and short susceptible, early maturing cultivars. They reported that negative correlations (r=-0.30) between heading date and resistance in F_2 population might suggest linkage. Early maturing (heading <110 days from seedling emergence), resistant plants were recovered in the F_2 population and continued expressing their resistance in succeeding generations.

Conversely, Bahat et al. (1980) reported no significant differences in disease severity between the susceptible cultivars that differed in plant maturity date. They found that number of infection cycles of the pathogen on a particular leaf may be greater on dwarf rather than on the semi-dwarf cultivars under low to moderate epidemics and under certain favorable environmental conditions.

Shaner et al. (1975) provided several explanations for the association between late maturity and leaf blotch severity. These included: a) septoria tritici blotch is a disease of cool, wet weather which is more likely to occur early in the growing season, and b) periods of greatest disease development seems to be from flowering through dough development, so that a cultivar that passes through these stages earlier is more likely to encounter cool weather. Thus, resistance might be an escape mechanism and in a genetic sense may be conditioned not by genes for "resistance", but by genes for delayed maturity. They also noted that physiological conditions associated with delayed senescence caused resistance, which is more or less independent of the weather. Also genes for resistance may be associated with late maturity through linkage, or are more strongly expressed in a late maturing wheat.

INHERITANCE OF RESISTANCE TO SEPTORIA TRITICI BLOTCH OF WHEAT

Heritable resistance to S. tritici has been clearly demonstrated based on reports by Shipton et al. (1971). However, genetic resistance to S. nodorum had not been demonstrated. The first experiment carried out to determine the nature of inheritance of resistance to septoria tritici blotch disease was reported in the late 1920's. Mackie (1929) found that resistance to this disease was inherited as a single recessive gene.

F_1, F_2, F_3, and backcross progenies of 'Nabob' (resistant) x 'Knox' and 'Vermillion' (susceptible) cultivars indicated that resistance to S. tritici was controlled by 2 independent, partially dominant genes which were additive in their effects (Narvaez et al. 1957). In F_1, F_2 and backcross progenies of 'Lerma 52' and 'P14' (resistant) x 'Lee' and 'Mayo 54' (susceptible) resistance was controlled by a single dominant gene.

In studies of the F_1, F_2, and backcross populations of 'Bulgaria 88' with three susceptible wheat cultivars, resistance to S. tritici in both seedling and mature plants was governed by a single dominant gene (Rillo et al. 1966). A high positive correlation between seedling and mature plant reaction to the disease was also reported by the same authors.

Inheritance of resistance to S. tritici in the cultivar 'Seabreeze' was found to be determined by at least three recessive genes (Rosielle et al. 1979). It was suggested that resistance in 'Veranopolis' and 'IAS-20' cultivars might be due to a single gene. Similar inheritance patterns found in 'Veranopolis' and 'IAS-20' and the common ancestry of these two cultivars indicated that they may carry the same gene for resistance.

Tolerance to S. tritici was reported to be governed by a small number of additive loci, and quite possibly by a single locus (Ziv et al. 1981).

A predominance of the single dominant mode of inheritance for resistance to S. tritici was reported by Wilson (1985). He also suggested that other modes of inheritance including duplicate dominant genes and a single incomplete dominant might be involved.

In an attempt to determine the inheritance of resistance to S. tritici Gough et al. (1985) studied 70 F_3 families from the cross between the winter wheat 'Velmorin' (resistant) x 'Chisholm' (susceptible). They reported three segregating groups as follows: 17 homozygous for resistance, 39 segregating for resistance and susceptibility, and 14 were homozygous for susceptibility. These numbers were a good fit (P= 0.5-0.7) for alleles segregating at a single locus.

Using F_1, F_2, and backcross between Bulgaria 88 (resistant) and Estanzuela Dolores (susceptible), Diaz et al. (1982) observed no qualitatively inherited patterns when determining the inheritance to septoria tritici blotch under conditions highly favorable to the disease. They found 177 resistant, 77 susceptible, and 57 intermediate plants in the F_2.

Among parental F_1, F_2, F_3 and backcross populations derived from crosses among spring and winter wheat cultivars in a complete diallel scheme, Danon et al. (1986) reported that resistance to S. tritici of the four winter wheats 'Aurora', 'Bezostaya 1', 'Kavkaz' and 'Trakia' to isolate ISR398 was controlled by one or two dominant genes. They reported there was no evidence for maternal effect on the expression of the disease coverage.

According to Van Ginkel (1986), the generation mean analysis applied among wheat crosses over generations clearly indicated the prime importance of additive gene effects in the inheritance of resistance to S. tritici followed by an enhanced effect by a dominance gene. Epistatic effects were quite rare, leading to both more confidence in the estimates obtained of additive and dominant gene effects and in the results of the combining ability analysis. The latter analysis indicated a major role for general combining ability. Specific combining ability estimates remained small, though often significant. This was probably due to the dominance gene and rare epistatic effects.

MATERIALS AND METHODS

Experimental material consisted of four isogenic lines of winter wheat (*T. aestivum* L.em Thell.), selected from the backcross population 'Itana'/3/'Norin 10'/'Brevor 14'//6*'Itana. Isogenic lines are represented by a two-gene short semidwarf CB11-77253 (Rht1Rht1Rht2Rht2); two one-gene medium semidwarf CB18-77262 (Rht1Rht1rht2rht2), or CB22-77267 (rht1rht1Rht2Rht2), and a standard height line CB23-77268 (rht1rht1rht2rht2). The isogenic lines are late maturing and moderate to resistant in response to septoria tritici blotch.

Tibet Dwarf extremely short statured, early maturing, and highly susceptible to septoria tritici blotch was used as the common parent in crosses with the isogenic lines. This selection was obtained in the Peoples Republic of China and named as 'Tibet Dwarf' by the cereal breeding program at Oregon State University.

Crosses were made using Tibet Dwarf as male and the four isogenic lines as female in the 1983-1984 crop cycle. In 1984-1985 the F_1 was advanced to F_2 generation. The parents, F_1, and F_2 were spaced planted on October 20, 1985 at the Hyslop Agronomy Farm. This site which is characterized by a fine, silty mixed mesic Aquultic Argixeroll soil type is located 11 km northeast of Corvallis, Oregon.

In the fall prior to planting, 67 kg/ha of Nitrogen and 8 kg/ha of sulfur were applied as 40-0-0-6. The fertility level was increased by the addition of 195 kg/ha of Nitrogen and 30 kg/ha of Sulfur in late Spring. An early application of Alachlor (2-chloro-N-(2,6-diethylphenil)-N-methoxymethylacetamide), and Chlorsulfuron (2-chloro-N-

[(4-methoxy-6-methyl-6-methyl-1,3,5-triazin-2-yl)aminocarbonyl]-benzenesulfonamide) were applied at a rate of 1.76 lt/ha and 23.35 gm/ha respectively for control of annual bluegrass (Poa annua).

A complete randomized split plot design with three replications was used. Crosses were used as the main plots. Parents and resulting F_1 and F_2 populations were used as subplots. Each treatment contained a single row of 15 plants with 15 cm between plants and 25 cm between rows. 'Stephens', a susceptible cultivar was planted around the blocks to provide a favorable spreader for S. tritici infection. Each plant in the trial was evaluated for five factors. These included:

1.-(PCD) = Percent coverage of disease in the uppermost four leaves at stage 11.3 of Feekes scale. In this particular study three septoria tritici blotch severity readings were made at stages 5, 10.1 and 11.3 of Feekes scale on a single plant basis over the uppermost four leaves and averaged.

2.-SPC = Septoria Progress Coefficient.

SPC = DISEASE HEIGHT (cm)/PLANT HEIGHT (cm), where:

DISEASE HEIGHT = The maximal height (cm) above the ground level at which the pycnidia of S. tritici could be found on plant tissue.

3.- PLANT HEIGHT was measured in cm. from the ground to the tip of the tallest spike of the plant when the plant was at stage 11.3 of Feekes scale.

4.- Heading date was recorded when the first spike on the plant emerged from the boot.

5.- Physiological maturity date was recorded when the main spike and peduncle lost their green color.

STATISTICAL ANALYSIS

The per plant values where averaged due to unequal sample sizes and the analysis of variance were conducted on the basis of plot means. However, for analysis of phenotypic correlation among plant height, heading and maturity date, and susceptibility to S. tritici the total of individual plant values was used.

GENETIC ANALYSIS

MINIMUM NUMBER OF SEGREGATING GENES IN THE F_2 GENERATION

The minimum number of segregating loci in the F_2 population was calculated employing the formula first described by Burton (1951, and 1966), later by Eyal (1982), and Van Ginkel (1986).

$$n = \frac{.25(.75 - h + h^2)D^2}{VF_2 - VF_1} \qquad h = \frac{F_1 - F_2}{P_2 - P_1} \qquad D = P_2 - P_1$$

WHERE:

P_1 = The mean of the smallest parent

P_2 = The mean of the largest parent

F_1 = The mean of the F_1 population and

F_2 = The mean of the F_2 population.

This formula will be valid only if:

1.- No linkage exists between pertinent genes.

2.- One parent supplies only plus factors and the other only minus factors among those in which they differ.

3.- All genes are equally important.

4.- The degree of dominance of plus factors is the same for all.

5.- No interaction exists between pertinent nonallelic genes.

DEGREE OF DOMINANCE AND GENE ACTION

THEORETICAL MEANS

$$\text{THEORETICAL ARITHMETIC } \bar{F}_1 = \frac{P_1 + P_2}{2}$$

$$\text{THEORETICAL ARITHMETIC } \bar{F}_2 = \frac{\bar{P}_1 + 2\bar{F}_1 + \bar{P}_2}{4}$$

$$\text{THEORETICAL GEOMETRIC } \bar{F}_2 = \text{ANTILOGARITHM OF } \frac{\log P_1 + 2\log F_1 + \log P_2}{4}$$

WHERE:

$\bar{P}_1$ = The mean of the smallest parent

$\bar{P}_2$ = The mean of the largest parent

$\bar{F}_1$ = The mean of the F_1 population

$\bar{F}_2$ = The mean of the F_2 population.

A comparison of the observed and calculated F_1 mean values were employed to reveal the possible nature and degree of dominance expressed in the inheritance of each character considered. The extent of the agreement between the observed and calculated F_2 means furnishes an indication of the nature of the gene action in the inheritance of each character in question (Burton 1951).

HERITABILITY PERCENTAGES

Heritability percentages in the broad sense were calculated for each character and cross by the following formula proposed by Burton (1951).

$$H = \frac{VF_2 - VF_1}{VF_2}$$

WHERE:

VF_2 = Variance of the F_2 population

VF_1 = Variance of the F_1 population

GENETIC CORRELATION

Genetic correlation was also obtained to measure possible heritable relationships for each variable studied. The following formula proposed by Burton (1951) was used:

$$\text{GENETIC CORRELATION} = \frac{cvXYF_2 - cvXYF_1}{\sqrt{(vXF_2 - vXF_1)(vYF_2 - vYF_1)}}$$

WHERE:

$cvXYF_2$ = Covariance of the F_2 of the two characters under study.

$cvXYF_1$ = Covariance of the F_1 of the two characters under study

$(vXF_2 - vXF_1)$ = Variance of the F_2 minus variance of the F_1 of the character X under study.

$(vYF_2 - vXF_1)$ = Variance of the F_2 minus variance of the F_1 of the character Y under study.

EXPERIMENTAL RESULTS

Results for parents, F_1 and F_2 generations of crosses between four isogenic lines with Tibet Dwarf, are divided into two sections. The first section identifies statistical differences in the experimental material while the second section focuses on genetic considerations.

STATISTICAL ANALYSIS

A. ANALYSIS OF VARIANCE.

Observed mean square values for plant height, percent coverage of disease (PCD), septoria progress coefficient (SPC), heading and maturity date are presented in Appendix Table 1.

Differences were observed for all factors measured for generations. For crosses differences were noted for all observations except days to heading. Interactions between crosses and generations were significant for plant height, PCD, and SPC.

Mean values, standard deviations and coefficients of variation for five characters observed for parents, F_1, and F_2 populations are provided in Appendix Table 2. Coefficients of variation were low for heading (1.2), and maturity date (0.8). Those for plant height (5.9), and PCD (10.6) were intermediate. The highest coefficient of variation present was noted for SPC (13.1).

B. PERFORMANCE OF PARENTS, F_1's, and F_2's FOR RESPONSE TO SEPTORIA TRITICI BLOTCH, PLANT HEIGHT AND HEADING DATE

The mean values for percent coverage of disease (PCD), septoria progress coefficient (SPC), plant height, and heading date for parents, F_1's, and F_2's are shown in Table 1.

Variability in the mean disease expression are apparent among the tall, semidwarf, and dwarf isogenic lines despite their common genetic background. Lowest mean values for the traits PCD (14.2 %), and SPC (0.18) were found for the semidwarf isogenic line rht_1Rht_2. The highest PCD (32.7 %), and SPC (0.69) mean values were observed for the dwarf isogenic line Rht_1Rht_2. Differences for plant height were also present. The tall isogenic line rht_1rht_2 was the tallest (131.4 cm), with the double dwarf Rht_1Rht_2 being the shortest (83.3 cm). Mean value differences for heading dates among the isogenic lines were small. The isogenic line rht_1rht_2 had the earliest heading date (145.3 days), while the semidwarf Rht_1rht_2 showed the latest (147.4 days). Tibet Dwarf had higher mean values when compared to the four isogenic lines for the traits PCD (55.6 %), and SPC (0.94). It also was 50 cm shorter in height compared to the double dwarf isogenic line Rht_1Rht_2. For heading date Tibet Dwarf was approximately 25 days earlier than the four isogenic lines.

The range for the five genotypes was 14.2 to 55.6 % for PCD, 0.18 to 0.94 for SPC, 34.7 to 131.4 cm for plant height, and 122.4 to 147.4 days for heading date.

Table 1. Mean values of percent coverage of disease (PCD), septoria progress coefficient (SPC), plant height, and heading date for five parents and resulting F_1 and F_2 populations grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

		(PCD) %	(SPC)	PLANT HEIGHT (cm)	HEADING DATE (DAYS)
PARENTS					
rht_1rht_2		21.6^{cd}\1	0.37^{d}	131.4^{a}	145.3^{b}
rht_1Rht_2		14.2^{d}	0.18^{e}	90.2^{c}	145.6^{b}
Rht_1rht_2		27.4^{bc}	0.46^{c}	111.7^{b}	147.4^{a}
Rht_1Rht_2		32.7^{b}	0.69^{b}	83.3^{c}	146.6^{ab}
TIBET DWARF		55.6^{a}	0.94^{a}	34.7^{d}	122.4^{c}
	MEAN	30.3	0.53	90.3	141.5
	RANGE	14.2-55.6	0.18-0.94	34.7-131.4	122.4-147.4
F_1'S					
rht_1rht_2 x TIBET		26.1^{b}	0.38^{b}	71.9^{a}	131.5^{a}
rht_1Rht_2 x TIBET		24.2^{b}	0.30^{c}	63.1^{b}	133.5^{a}
Rht_1rht_2 x TIBET		44.3^{a}	0.78^{a}	60.4^{bc}	131.7^{a}
Rht_1Rht_2 X TIBET		41.5^{a}	0.75^{a}	56.6^{c}	132.8^{a}
	MEAN	34.0	0.55	63.0	132.4
	RANGE	24.2-44.3	0.30-0.78	60.4-71.9	131.5-133.7
F_2'S					
rht_1rht_2 x TIBET		31.5^{c}	0.51^{c}	72.9^{a}	134.8^{a}
rht_1Rht_2 x TIBET		34.6^{b}	0.55^{bc}	64.4^{b}	135.3^{a}
Rht_1rht_2 x TIBET		41.6^{a}	0.71^{a}	71.3^{a}	133.2^{a}
Rht_1Rht_2 x TIBET		36.4^{b}	0.62^{b}	61.7^{c}	136.9^{a}
	MEAN	36.0	0.60	67.6	135.0
	RANGE	31.5-41.6	0.51-0.71	61.7-72.9	133.2-136.9

\1 = Genotypes denoted by the same letter in the same column are not significantly different at 0.05 level using LSD.

Among the F_1's the combination Rht_1rht_2 x Tibet Dwarf showed the highest population mean value for both PCD, and SPC. The F_1 from the cross between rht_1Rht_2 x Tibet Dwarf had the lowest PCD, and SPC mean values. The F_2 population resulting from Rht_1rht_2 x Tibet Dwarf cross again had the highest PCD, and SPC mean values. Combination between rht_1rht_2 x Tibet Dwarf showed the lowest values. There was close agreement of the F_2 population mean values for PCD between rht_1Rht_2, and Rht_1Rht_2 x Tibet Dwarf.

The F_1 and F_2 rht_1rht_2 x Tibet Dwarf presented the higher mean values for plant height with the F_1 and F_2 populations involving Rht_1Rht_2 x Tibet Dwarf being the shortest. Earliest heading date mean values for the F_1 and F_2 population were manifested in crosses between rht_1rht_2, and Rht_1rht_2 x Tibet Dwarf, respectively. The F_1 from rht_1Rht_2 x Tibet Dwarf, and F_2 from Rht_1Rht_2 x Tibet Dwarf presented the latest heading date mean values, although the differences were not significant.

The range for the F_1's was 24.2 to 44.3 % for PCD, 0.30 to 0.78 for SPC, 60.4 to 71.9 cm for plant height, and 131.5 to 133.7 days for heading date. The range for the F_2's was 31.5 to 41.6 for PCD, 0.51 to 0.71 for SPC, 61.7-72.9 cm for plant height, and 133.2 to 136.9 days for heading date.

An orthogonal contrast mean analysis, F values and probability level for percent coverage of disease (PCD), septoria progress coefficient (SPC), plant height, and heading date for the isogenic lines, F_1 and F_2 populations are shown in Tables 2 through 5 respectively.

Table 2. Orthogonal mean analysis of percent coverage of disease (PCD) for four isogenic lines, F_1, and F_2 populations grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

GENERATION	Isogenic Line (P_1)			
	rht_1rht_2	Rht_1rht_2	rht_1Rht_2	Rht_1Rht_2
	(PCD %)			
P1	32.7	27.4	14.2	32.7
Progenies:				
F_1	26.1	44.3	24.2	41.5
F_2	31.5	41.6	34.6	36.4
Susceptible parent (P_2):				
Tibet Dwarf	55.6			

Generation P_1 :
F = 7.33; Probability > F = 0.0197
Contrast crosses to Rht_1 vs Rht_2
F = 10.04; Probability > F = 0.0194
Contrast crosses to Rht_1 and Rht_2 vs Rht_1Rht_2
F = 11.02; Probability > F = 0.0160

F_1 :
F = 18.59; Probability > F = 0.0019
Contrast crosses to Rht_1 vs Rht_2
F = 37.03; Probability > F = 0.0009
Contrast crosses to Rht_1 and Rht_2 vs Rht_1Rht_2
F = 6.30; Probability > F = 0.0459
Contrast crosses to rht_1rht_2 vs crosses to all other isogenic lines:
F = 12.45; Probability > F = 0.0124

F_2 :
F = 33.11; Probability > F = 0.0004
Contrast crosses to Rht_1 vs Rht_2
F = 45.34; Probability > F = 0.0005
Contrast crosses to rht_1rht_2 vs crosses to all other isogenic lines:
F = 50.58; Probability > F = 0.0004

Table 3. Orthogonal mean analysis of septoria progress coefficient (SPC) for four isogenic lines, F_1, and F_2 populations grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

GENERATION	Isogenic Line (P_1) rht_1rht_2	Rht_1rht_2 (SPC)	rht_1Rht_2	Rht_1Rht_2
P1	0.37	0.46	0.18	0.69
Progenies:				
F_1	0.38	0.78	0.30	0.75
F_2	0.51	0.71	0.55	0.62
Susceptible parent (P_2):				
Tibet Dwarf	0.94			

Generation P_1 : $F = 7.42$; Probability > F = 0.0192
Contrast crosses to Rht_1 vs Rht_2
$F = 6.28$; Probability > F = 0.0461
Contrast crosses to Rht_1 and Rht_2 vs Rht_1Rht_2
$F = 15.87$; Probability > F = 0.0073

F_1 : $F = 77.97$; Probability > F = 0.0001
Contrast crosses to Rht_1 vs Rht_2
$F = 148.07$; Probability > F = 0.0001
Contrast crosses to Rht_1 and Rht_2 vs Rht_1Rht_2
$F = 42.88$; Probability > F = 0.0006
Contrast crosses to rht_1rht_2 vs crosses to all other isogenic lines:
$F = 42.95$; Probability > F = 0.0006

F_2 : $F = 14.14$; Probability > F = 0.0040
Contrast crosses to Rht_1 vs Rht_2
$F = 23.85$; Probability > F = 0.0028
Contrast crosses to rht_1rht_2 vs crosses to all other isogenic lines:
$F = 18.46$; Probability > F = 0.0051

Table 4. Orthogonal mean analysis of plant height for four isogenic lines, F_1, and F_2 populations grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	Isogenic Line (P_1)			
GENERATION	rht_1rht_2	Rht_1rht_2	rht_1Rht_2	Rht_1Rht_2
	PLANT HEIGHT			
P1	131.4	111.7	90.2	83.3
Progenies:				
F_1	71.9	60.4	63.1	56.6
F_2	72.9	71.3	64.4	61.7
Short parent (P_2):				
Tibet Dwarf	34.7			

Generation P_1 : F = 39.18; Probability > F = 0.0002
Contrast crosses to Rht_1 vs Rht_2
F = 19.31; Probability > F = 0.0046
Contrast crosses to Rht_1 and Rht_2 vs Rht_1Rht_2
F = 16.79; Probability > F = 0.0064
Contrast crosses to rht_1rht_2 vs crosses to all other isogenic lines:
F = 81.44; Probability > F = 0.0001

F_1 : F = 16.67; Probability > F = 0.0026
Contrast crosses to Rht_1 and Rht_2 vs Rht_1Rht_2
F = 7.34; Probability > F = 0.0351
Contrast crosses to rht_1rht_2 vs crosses to all other isogenic lines:
F = 40.92; Probability > F = 0.0007

F_2 : F = 2.65; Probability > F = 0.1430

Table 5. Orthogonal mean analysis of heading date for four isogenic lines, F_1, and F_2 populations grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	Isogenic Line (P_1)			
GENERATION	rht_1rht_2	Rht_1rht_2	rht_1Rht_2	Rht_1Rht_2
	HEADING DATE			
P1	145.3	147.4	145.6	146.6
Progenies:				
F_1	131.5	131.7	133.5	132.8
F_2	134.8	133.2	135.3	136.9
Early parent (P_2):				
Tibet Dwarf	122.4			

Generation P_1 : F = 4.76; Probability > F = 0.0499
Contrast crosses to Rht_1 vs Rht_2
F = 8.13; Probability > F = 0.0292
Contrast crosses to rht_1rht_2 vs crosses to all other isogenic lines:
F = 6.12; Probability > F = 0.0483

F_1 : F = 1.09; Probability > F = 0.4214

F_2 : F = 1.62; Probability > F = 0.2802

Results presented in Tables 2 and 3 suggest that both percent coverage of disease (PCD) and septoria progress coefficient (SPC) gave similar response in measuring septoria tritici blotch severity. Differences were found for parents, F_1, and F_2 population for PCD and SPC when comparing the two single semidwarf genes Rht_1 vs Rht_2 (Table 2 and 3 respectively). A similar response was found for the contrast Rht_1 and Rht_2 vs Rht_1Rht_2 together for the isogenic lines and F_1 population. When comparing rht_1rht_2 vs Rht_1, Rht_2, or Rht_1Rht_2 differences where present for the F_1 and F_2 populations.

Significant differences for plant height were observed when comparing Rht_1 vs Rht_2, Rht_1 and Rht_2 vs Rht_1Rht_2, and rht_1rht_2 vs Rht_1, Rht_2 or Rht_1Rht_2 for the isogenic lines (Table 4). Differences where also found among the F_1's when the single genes Rht_1 and Rht_2 where compared with both genes together Rht_1Rht_2. However, no differences among the F_2's were detected.

Results in Table 5 for heading date indicated that small differences were present for this trait. Differences were found among the isogenic lines when comparing Rht_1 vs Rht_2, and rht_1rht_2 vs all other isogenic lines. However, there were no differences among the F_1 or F_2 populations.

GENETIC ANALYSIS

The response to septoria tritici blotch by F_1 and F_2 populations in this section was measured using only the percent coverage of disease (PCD). In addition, results for F_1 and F_2 populations for plant height and heading date are presented to evaluate the possible association of these two traits on the development of the disease.

A. PERFORMANCE IN F_1 GENERATION FOR SEPTORIA TRITICI BLOTCH, PLANT HEIGHT, AND HEADING DATE

Mean values of percent coverage of disease (PCD) for four F_1 populations are compared with their parents in Table 6a. Among the F_1's the combination of rht_1Rht_2 x Tibet Dwarf showed the lowest percent coverage of disease (24.17 %). Crosses between Rht_1rht_2 x Tibet Dwarf showed the highest F_1 mean percent coverage of disease value (44.36 %).

F_1 populations were intermediate in their reaction to septoria tritici blotch when compared to the midparent values. All combinations of F_1's were less susceptible than the midparent values except in the F_1 resulting from Rht_1rht_2 x Tibet Dwarf. There was partial dominance for resistance for the F_1's between rht_1rht_2, and rht_1Rht_2 x Tibet Dwarf. The F_1's, Rht_1rht_2, and Rht_1Rht_2 x Tibet Dwarf were similar to their respective midparent values suggesting incomplete dominance.

Mean values of the F_1's, for plant height are compared with their respective parents in Table 6b. Among the F_1's, the cross isogenic line rht_1rht_2 x Tibet Dwarf was the tallest, with the F_1 between the semidwarf Rht_1Rht_2 x Tibet Dwarf being the shortest. All F_1's were intermediate in height compared to their parents. They were, however, shorter than their respective midparent values except in the F_1 rht_1Rht_1 x Tibet Dwarf. Thus, the F_1 populations varied from incomplete to partial dominance favoring short stature.

TABLE 6a. Mean values for severity to septoria tritici blotch for parents and four F_1 populations grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

CROSS	F_1	RESISTANT PARENT	SUSCEPTIBLE PARENT	MIDPARENT
Rht_1rht_2 x TIBET DWARF	44.36[a]\1	27.40[b]	55.60[a]	41.50
Rht_1Rht_2 x TIBET DWARF	41.46[b]	32.67[a]	55.34[a]	44.00
rht_1rht_2 TIBET DWARF	26.09[c]	21.60[c]	55.51[a]	38.60
rht_1Rht_2 x TIBET DWARF	24.17[c]	14.15[d]	54.84[a]	34.50

\1 = F_1's and parents denoted by the same letter in the cross column are not significantly different at 0.05 level using LSD method.

TABLE 6b. Mean values for plant height for parents and four F_1 populations grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

CROSS	F_1	TALL PARENT	SHORT PARENT	MIDPARENT
rht_1rht_2 x TIBET DWARF	71.90[a]\1	131.36[a]	34.29[a]	82.82
rht_1Rht_2 x TIBET DWARF	63.13[b]	90.24[c]	34.42[a]	62.33
Rht_1rht_2 TIBET DWARF	60.42[c]	111.67[b]	35.18[a]	73.42
Rht_1Rht_2 x TIBET DWARF	56.58[c]	83.33[d]	34.93[a]	59.13

\1 = F_1'S and parents denoted by the same letter in the cross column are not significantly different at 0.05 level using LSD method.

TABLE 6c. Mean values for heading date for parents and four F_1 populations grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

CROSS	F_1	EARLY PARENT	LATE PARENT	MIDPARENT
rht_1Rht_2 x TIBET DWARF	133.5[ab]\1	123.3[a]	145.6[ab]	134.5
Rht_1Rht_2 x TIBET DWARF	132.8[b]	122.9[a]	146.6[ab]	134.8
rht_1rht_2 TIBET DWARF	131.5[b]	120.5[a]	145.3[b]	132.9
Rht_1rht_2 x TIBET DWARF	131.7[b]	123.0[a]	147.4[a]	135.2

\1 = F_1'S and parents denoted by the same letter in the cross column are not significantly different at 0.05 level using LSD method.

Mean values for the F_1's involving heading date are compared with their parents in Table 6c. The cross Rht_1rht_2 x Tibet Dwarf was earliest in heading with the F_1 between rht_1Rht_2 x Tibet Dwarf being the latest population to head. All F_1's were intermediate in heading when compared to their parents. The F_1's were earlier than their midparent values. There was a general tendency toward partial dominance for early heading date.

B. PERFORMANCE IN F_2 GENERATION FOR SEPTORIA TRITICI BLOTCH, PLANT HEIGHT, AND HEADING DATE

No discrete classes were observed among individuals in the F_2 generation for the character percent coverage of disease (PCD). Thus, no qualitative analysis was applied for this factor when determining the mode of inheritance.

The data in Table 7a reveal that the F_2 mean for percent coverage of disease between the tall isogenic line rht_1rht_2 x Tibet Dwarf was intermediate between the two parents. The frequency distribution of the F_2 suggests that individual plant types were recovered with reactions similar to both the susceptible and resistant parents. Considering the range of the parents, a greater number of plants with reactions similar to the resistant parent were recovered. The higher standard deviation of the F_2 when compared to the F_1 suggests that considerable genetic variation was present for disease reaction. The range of the F_2 also indicates that transgressive segregation toward resistance was present in this cross.

Table 7a. Frequency distribution, range, mean, and standard deviation of percent coverage of disease (PCD) for parents, F_1, and F_2 from cross rht_1rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	CLASSES (PCD)								
	A	B	C	D	E				
GENERATION	5-15\1	15-25	25-35	35-45	> 45	N\2	RANGE	MEAN	STANDARD DEVIATION
rht_1rht_2	17	6	21			44	11.0-33.7	21.6[c]\3	9.68
TIBET DWARF					42	42	52.0-59.7	55.1[a]	6.86
F_1		13	5	1		19	21.7-34.3	26.1[bc]	5.25
F_2	14	58	29	48	31	180	1.0-57.7	31.5[b]	12.95

\1 = Classification of parents, F_1, and F_2 to severity classes (A-E) based on percent coverage of pycnidia of S. tritici.

\2 = N = Total number of plants.
\3 = Mean values denoted by the same letter are not significantly different at 0.05 level using LSD method.

Table 7b. Frequency distribution, range, mean, and standard deviation of percent coverage of disease (PCD) for parents, F_1, and F_2 from cross rht_1Rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	CLASSES (PCD)								
	A	B	C	D	E				
GENERATION	5-15\1	15-25	25-35	35-45	> 45	N\2	RANGE	MEAN	STANDARD DEVIATION
rht_1Rht_2	15	26				41	8.3-20.0	14.2[d]\3	4.90
TIBET DWARF					41	41	51.7-60.0	57.9[a]	6.20
F_1		5	3			8	21.3-30.3	24.2[c]	3.05
F_2	3	34	42	38	56	173	1.0-55.6	34.6[b]	11.40

\1 = Classification of parents F_1, and F_2 to severity classes (A-E) based on percent coverage of pycnidia of S. tritici.

\2 = N = Total number of plants.

\3 = Mean values denoted by the same letter are not significantly different at 0.05 level using LSD method.

Similar F_2 mean values for percent coverage of disease were observed between rht_1Rht_2, and Rht_1Rht_2 x Tibet Dwarf (Tables 7b, and 7c). Mean F_2 values for these crosses were intermediate between the two parents. Transgressive segregation toward resistance was observed in the F_2 population between rht_1Rht_2 x Tibet Dwarf (Table 7b). The range of the F_2 indicates that resistant plants with 1 % levels of infection were present. The standard deviation of the F_2's in both crosses were higher than that of the F_1 populations indicating both environmental and genetic variation were present.

Data presented for percent coverage of disease in Table 7c between Rht_1Rht_2 x Tibet Dwarf is not easily interpreted. The F_2 mean value was lower than the F_1. Although the frequency distribution of the F_2 indicated that a great number of plants were susceptible to the disease, it seems probable that the presence of the rht_1Rht_2 dwarf gene is conferring some resistance. Thus, the range of the F_2 reflects that resistant plants with levels of infection lower than 15 % were present in this population.

Table 7d shows that the F_2 between Rht_1rth_2 x Tibet Dwarf was more closely related to the susceptible parent. This is in agreement with the F_1 mean values. The frequency of the F_2 indicated that plants in class A (5-15) considered as resistant in this study were not recovered. A large number of susceptible plants with PCD higher than 45 % were observed. Note, however, that the range of the resistant parent fell between classes B and D. Results in this cross might suggest that the rht_2 gene is not associated with resistance. This is supported by the high population PCD mean values for the F_1 (44.3), and F_2 (41.6).

Table 7c. Frequency distribution, range, mean, and standard deviation of percent coverage of disease (PCD) for parents, F_1, and F_2 from cross Rht_1Rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	CLASSES (PCD)								
	A	B	C	D	E				
GENERATION	5-15\1	15-25	25-35	35-45	> 45	N\2	RANGE	MEAN	STANDARD DEVIATION
Rht_1Rht_2			45			45	24.7-31.7	32.7[d]\3	3.23
TIBET DWARF					42	42	49.3-59.0	55.6[a]	2.87
F_1			1	13	5	19	31.0-48.3	41.5[b]	4.50
F_2	4	30	28	55	58	175	10.3-55.3	36.4[c]	11.11

\1 = Classification of parents, F_1, and F_2 to severity classes (A-E) based on percent coverage of pycnidia of *S. tritici*.

\2 = N = Total number of plants.

\3 = Mean values denoted by the same letter are not significantly different at 0.05 level using LSD method.

Table 7d. Frequency distribution, range, mean, and standard deviation of percent coverage of disease (PCD) for parents, F_1, and F_2 from cross Rht_1rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	CLASSES (PCD)								
	A	B	C	D	E				
GENERATION	5-15\1	15-25	25-35	35-45	> 45	N\2	RANGE	MEAN	STANDARD DEVIATION
Rht_1rht_2		7	30	8		45	24.7-31.7	27.4c\3	3.23
TIBET DWARF					44	44	51.0-62.7	55.3a	3.73
F_1			1	9	28	38	34.7-55.3	44.3b	3.38
F_2	0	12	12	35	113	185	16.0-58.7	41.6b	10.42

\1 = Classification of parents, F_1, and F_2 to severity classes (A-E) based on percent coverage of pycnidia of *S. tritici*.

\2 = N = Total number of plants.

\3 = Mean values denoted by the same letter are not significantly different at 0.05 level using LSD method.

Table 8. Observed and calculated means, number of genes in the F_2, and heritability estimates for Septoria severity in crosses involving four isogenic lines and Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

		F_2 POPULATION MEANS			
CROSS	OBSERVED MEAN	CALCULATED MEAN ARITHMETIC\1	CALCULATED MEAN GEOMETRIC\2	NUMBER OF GENES IN THE F_2	"HERITABILITY"
Rht_1Rht_2 x TIBET DWARF	36.35^{b}\3	42.79	42.04	0.28	0.84
Rht_1rht_2 x TIBET DWARF	41.56^{a}	42.85	41.55	0.43	0.90
rht_1Rht_2 x TIBET DWARF	34.56^{b}	30.08	26.29	1.85	0.93
rht_1rht_2 x TIBET DWARF	31.50^{c}	32.22	30.00	1.20	0.84

\1 = ARITHMETIC MEAN = $\dfrac{\bar{P}_1 + 2\bar{F}_1 + \bar{P}_2}{4}$

\2 = GEOMETRIC MEAN = Antilog $\dfrac{\log\bar{P}_1 + 2\log\bar{F}_1 + \log\bar{P}_2}{4}$

\3 = F_2's denoted by the same letter are not statistically different at 0.05 level using LSD method.

Results for observed and calculated arithmetic and geometric means, estimated gene number, gene action, and heritability estimates for septoria tritici blotch severity measured as percent coverage of disease (PCD) are presented in Table 8.

Comparison of the F_2 observed mean values for PCD indicates the observed means for the crosses between rht_1rht_2 and rht_1Rht_2 x Tibet Dwarf were near the population arithmetic means. The F_2 between the semidwarf Rht_1rht_2 x Tibet Dwarf was close to their geometric mean. Therefore, additive gene action for PCD seems more probable for the F_2 populations between rht_1rht_2, and rht_1Rht_2 x Tibet Dwarf, and non-additive type of gene action for the cross Rht_1rht_2 x Tibet Dwarf. However, neither calculated F_2 mean agrees with the observed mean for the F_2 population between Rht_1Rht_2 x Tibet Dwarf. Therefore, the nature of gene action can not be ascertained for this cross.

Estimated segregating genes in the F_2 were low in all four crosses suggesting one or two genes were governing resistance to septoria tritici blotch. Likewise the heritability values in the broad sense were high for all four crosses. The highest heritability estimate was obtained for the combination between rht_1Rht_2 x Tibet Dwarf 0.93, followed by Rht_1rht_2 x Tibet Dwarf with 0.90. Similar heritability estimates were observed for the combinations Rht_1Rht_2, and rht_1rht_1 x Tibet Dwarf with 0.84 for both crosses.

The frequency distribution of plant height for the four crosses is shown in Appendix Figures 1 through 4. The clear discrete classes among individuals in the F_2 populations suggest that plant height is qualitatively inherited in these crosses.

Table 9a. Frequency distribution, range, mean and standard deviation of plant height for parents, F_1, and F_2 from cross Rht_1rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	CLASSES PLANT HEIGHT											
	A	B	C	D	E	F	G	H				
GENERATION	30-40[1]	40-50	50-60	60-70	70-80	80-90	90-100	> 100	N[2]	RANGE	MEAN	STANDARD DEVIATION
Rht_1rht_2								45	45	105 - 115	111.7^{a}[3]	4.77
TIBET DWARF	44								44	32 - 37	35.2^{d}	0.76
F_1			31	7					38	58 - 64	60.4^{c}	1.15
F_2	36	15	43	19	7	12	15	38	185	25 - 135	71.3^{b}	27.92

\1 = Classification of parents, F_1, and F_2 to different plant height classes (A-H).
\2 = N = Total number of plants.
\3 = Mean values denoted by the same letter are not significantly different at 0.05 level using LSD method.

Table 9b. Frequency distribution, range, mean, and standard deviation of plant height for parents, F_1, and F_2 from cross rht_1rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	CLASSES PLANT HEIGHT											
	A	B	C	D	E	F	G	H				
GENERATION	30-40\1	40-50	50-60	60-70	70-80	80-90	90-100	> 100	N\2	RANGE	MEAN	STANDARD DEVIATION
rht_1rht_2								44	44	125 - 140	131.4^{a}\3	6.32
TIBET DWARF	42								42	30 - 36	34.3^{c}	1.33
F_1				11	8				19	70 - 75	71.9^{b}	2.38
F_2	26	21	24	45	8	5	11	40	180	30 - 135	72.9^{b}	26.88

\1 = Classification of parents, F_1, and F_2 to different plant height classes (A-H).
\2 = N = Total number of plants.
\3 = Mean values denoted by the same letter are not significantly different at 0.05 level using LSD method.

Similar frequency distributions were observed for plant height for all four crosses. The mean plant height on F_2 plants was intermediate between that of the parents and similar to the mean values of the F_1's, except for the cross between Rht_1rht_2 x Tibet Dwarf, where the F_1 and F_2 mean values differ by 11 cm (Table 9a). Plants taller than the tall parent were observed in the F_2 population between rht_1Rht_2, Rht_1rht_2, and $Rht1Rht_2$ x Tibet Dwarf. Therefore, transgressive segregation toward plant height was present for these crosses. However, there was no evidence for transgressive segregation in the F_2 between rht_1rht_2 x Tibet Dwarf. The range for this cross fell between the two parents (Table 9b). The standard deviations were high for all four crosses indicating genetic variation was present among individuals in the F_2. The lowest standard deviation was observed in the F_2 Rht_1Rht_2 x Tibet Dwarf 18.07 (Table 9c), followed by the F_2 between rht_1Rht_2 x Tibet Dwarf 19.49 (Table 9d). The highest standard deviations were observed for the F_2's between rht_1rht_2 and Rht_1rht_2 x Tibet Dwarf with 27.92 and 26.88, respectively.

All combinations produced a number of grass clumps which were shorter than the short parent in the F_2 generations. Nevertheless, these grass clumps were not considered in determining the nature of inheritance of plant height. A summary of grass clumps present for each F_2 population is presented in Appendix Table 3.

The F_2 observed mean values for plant height are compared with their calculated arithmetic and geometric means in Table 10. All F_2 observed means were near their arithmetic means except the F_2 population between rht_1rht_2 x Tibet Dwarf, which was found related to the geometric mean.

Table 9c. Frequency distribution, range, mean, and standard deviation of plant height for parents, F_1, and F_2 from cross Rht_1Rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	CLASSES PLANT HEIGHT											
	A	B	C	D	E	F	G	H				
GENERATION	30-40\1	40-50	50-60	60-70	70-80	80-90	90-100	> 100	N\2	RANGE	MEAN	STANDARD DEVIATION
Rht_1Rht_2					15	30			45	80 - 85	83.3^{a}\3	2.38
TIBET DWARF	42								42	32 - 35	34.9^{d}	0.46
F_1			19						19	55 - 60	56.6^{c}	2.39
F_2	23	43	40	23	19	14	10	3	175	35 - 105	61.7^{b}	18.07

\1 = Clasification of parents, F_1, and F_2 to different plant height classes (A-H).
\2 = N = Total number of plants.
\3 = Mean values denoted by the same letter are not significantly different at 0.05 level using LSD method.

Table 9d. Frequency distribution, range, mean, and standard deviation of plant height for parents, F_1, and F_2 from cross rht_1Rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	CLASSES PLANT HEIGHT											
	A	B	C	D	E	F	G	H				
GENERATION	30-40\1	40-50	50-60	60-70	70-80	80-90	90-100	> 100	N\2	RANGE	MEAN	STANDARD DEVIATION
rht_1Rht_2						26	15		41	85 - 95	90.2[a]\3	4.18
TIBET DWARF	41								41	30 - 35	34.4[c]	1.23
F_1			5	3					8	60 - 65	63.1[b]	2.59
F_2	16	31	63	9	17	16	15	6	173	30 - 120	64.4[b]	19.49

\1 = Classification of parents, F_1, and F_2 to different plant height classes (A-H).
\2 = N = Total number of plants.
\3 = Mean values denoted by the same letter are not significantly different at 0.05 level using LSD method.

Table 10. Observed and calculated means, number of genes in the F_2, and heritability estimates for plant height in crosses involving four isogenic lines and Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

		F_2 POPULATION MEANS			
CROSS	OBSERVED MEAN	CALCULATED MEANS ARITHMETIC\1	GEOMETRIC\2	NUMBER OF GENES IN THE F_2	"HERITABILITY"
rht_1rht_2 x TIBET DWARF	72.86[a]\3	77.36	69.25	0.70	0.99
Rht_1rht_2 x TIBET DWARF	71.32[a]	66.92	61.54	0.59	0.99
rht_1Rht_2 x TIBET DWARF	64.36[b]	63.98	51.66	0.13	0.90
Rht_1Rht_2 x TIBET DWARF	61.66[c]	57.86	55.25	0.19	0.98

\1 = ARITHMETIC MEAN = $\dfrac{\overline{P}_1 + 2\overline{F}_1 + \overline{P}_2}{4}$

\2 = GEOMETRIC MEAN = Antilog $\dfrac{\log\overline{P}_1 + 2\log\overline{F}_1 + \log\overline{P}_2}{4}$

\3 = F_2's denoted by the same letter are not statistically different at 0.05 level using LSD method.

Therefore, additive gene action seems more probable for plant height in these crosses, except for the combination between rht_1rht_2 x Tibet Dwarf where non-additive type of gene action was also determining plant height. The number of segregating genes in all four F_2 populations was low suggesting that one or two genes were involved for plant height. The heritability estimates were high for all four combinations. The lowest heritability estimate in the broad sense was obtained for rht_1Rht_2 x Tibet Dwarf 0.90. Slight differences were present among the other crosses whose heritability estimates were above 0.98.

The frequency distributions for heading date are presented in Appendix Figures 5 through 8. Discrete classes among individuals in the F_2 generations were observed suggesting that the action of major genes were involved in determining heading date.

Similar response was observed among the F_2 populations for the four crosses. The mean heading date of the F_2 generation was intermediate between that of the parents which was in agreement with the mean values of the F_1's. Transgressive segregation was observed toward both early and late heading in all four F_2 populations.

Table 11a indicates that the number of plants heading earlier than the earliest parent was relatively low for the F_2 between rht_1rht_2 x Tibet Dwarf. A similar heading response was observed for the F_2's between rht_1Rht_2 and Rht_1Rht_2 x Tibet Dwarf (Tables 11b and 11c respectively). A large number of early heading plants was found for the F_2 between Rht_1rht_2 x Tibet Dwarf (Table 11d). However, a number of late plants in the F_2 from Rht_1Rht_2 x Tibet Dwarf cross were observed (Table 11c).

Table 11a. Frequency distribution, range, mean, and standard deviation of heading date for parents, F_1, and F_2 from cross rht_1rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	CLASSES HEADING DATE								
	A	B	C	D	E				
GENERATION	114-120\1	122-128	130-136	138-144	146-152	N\2	RANGE	MEAN	STANDARD DEVIATION
rht_1rht_2					44	44	145-146	145.3[a]\3	0.48
TIBET DWARF		42				42	116-123	120.5[c]	3.37
F_1			19			19	130-132	131.5[b]	0.91
F_2	3	37	57	65	18	180	116-149	134.8[b]	7.11

\1 = Classification of parents, F_1, and F_2 to different heading date classes (A-E).
\2 = N = Total number of plants.
\3 = Mean values denoted by the same letter are not significantly different at 0.05 level using LSD method.

Table 11b. Frequency Distribution, range, mean, and standard deviation of heading date for parents, F_1, and F_2 from cross rht_1Rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	CLASSES HEADING DATE								
	A	B	C	D	E				
GENERATION	114-120\1	122-128	130-136	138-144	146-152	N\2	RANGE	MEAN	STANDARD DEVIATION
rht_1Rht_2					41	41	145-147	145.6^{a}\3	0.94
TIBET DWARF		41				41	121-127	123.4^{c}	1.43
F_1			8			8	132-135	133.5^{b}	1.31
F_2	3	26	62	64	18	173	117-157	135.0^{b}	6.88

\1 = Classification of parents, F_1, and F_2 to different heading date classes (A-E).
\2 = N = Total number of plants.
\3 = Mean values denoted by the same letter are not significantly different at 0.05 level using LSD method.

Table 11c. Frequency Distribution, range, mean, and standard deviation of heading date for parents, F_1, and F_2 from cross Rht_1Rht_2 x Tibet Dwarf grown at the Hyslop Farm. Corvallis, Oregon, 1985-1986.

	CLASSES HEADING DATE								
	A	B	C	D	E				
GENERATION	114-120\1	122-128	130-136	138-144	146-152	N\2	RANGE	MEAN	STANDARD DEVIATION
Rht_1Rht_2					45	45	146-147	146.7[a]\3	0.48
TIBET DWARF		42				42	121-123	122.9[c]	2.87
F_1			19			19	132-133	132.8[b]	0.48
F_2	1	17	61	64	32	175	118-150	136.9[b]	6.61

\1 = Classification of parents, F_1, and F_2 to different heading date classes (A-E).
\2 = N = Total number of plants.
\3 = Mean values denoted by the same letter are not significantly different at 0.05 level using LSD method.

Table 11d. Frequency distribution, range, mean, and standard deviation of heading date for parents, F_1, and F_2 from cross Rht_1rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

	CLASSES HEADING DATE								
	A	B	C	D	E				
GENERATION	114-120\1	122-128	130-136	138-144	146-152	N\2	RANGE	MEAN	STANDARD DEVIATION
Rht_1rht_2					45	45	147-149	144.4[a]\3	0.86
TIBET DWARF		44				44	121-125	123.0[c]	1.01
F_1			38			38	130-133	131.7[b]	1.27
F_2	13	25	67	66	14	185	114-150	133.2[b]	7.62

\1 = Classification of parents, F_1, and F_2 to different heading date classes (A-E).
\2 = N = Total number of plants.
\3 = Mean values denoted by the same letter are not significantly different at 0.05 level using LSD method.

Table 12. Observed and calculated means, number of genes in the F_2, and heritability estimates for heading date in crosses involving four isogenic lines and Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon. 1985-1986.

	F_2 POPULATION MEANS				
CROSS	OBSERVED MEAN	CALCULATED MEAN ARITHMETIC\1	GEOMETRIC\2	NUMBER OF GENES IN THE F_2	"HERITABILITY"
Rht_1Rht_2 TIBET DWARF	136.9[a]\3	133.8	133.6	0.55	0.99
rht_1Rht_2 x TIBET DWARF	135.3[a]	134.0	133.9	0.24	0.96
rht_1rht_2 x TIBET DWARF	134.8[a]	132.2	131.9	0.35	0.98
Rht_1rht_2 x TIBET DWARF	133.2[a]	133.5	133.3	0.80	0.99

\1 = ARITHMETIC MEAN = $\frac{\bar{P}_1 + 2\bar{F}_1 + \bar{P}_2}{4}$

\2 = GEOMETRIC MEAN = Antilog $\frac{\log\bar{P}_1 + 2\log\bar{F}_1 + \log\bar{P}_2}{4}$

\3 = F_2's denoted by the same letter are not statistically different at 0.05 level using LSD method.

Similar findings were not present in other F_2 populations. The standard deviations for all four F_2's were relatively high when compared to the standard deviations of their F_1's, indicating genetic variability existed between individuals in the F_2 populations.

The F_2 observed mean values are compared with their calculated arithmetic and geometric means in Table 12. All observed F_2 values were more related to their arithmetic means for this trait. Therefore, additive gene action is suggested for heading date in these crosses. Number of segregating genes in all four F_2 populations was low indicating that one or two genes were involved in determining heading date. The heritability estimates for this trait were above 0.95 for all four crosses.

ASSOCIATIONS AMONG SEPTORIA TRITICI BLOTCH, SEPTORIA PROGRESS COEFFICIENT, PLANT HEIGHT, AND HEADING AND MATURITY DATE

A.- TEST FOR INDEPENDENCE.

The frequency distribution of the F_2 population for plant height presented in Appendix Figures 1 through 4 indicates that three different classes could be observed for the four crosses, short (0-50 cm), semidwarf (50-90 cm), and tall (> 90 cm). Within each plant height class three levels of resistance were categorized according to their response to septoria progress coefficient (SPC): a) resistant SPC < 0.25, b) moderate resistance SPC = 0.25-0.50, and c) susceptible SPC > 0.50. The data obtained to test the association between septoria tritici blotch within different plant height class and Chi-square values are presented in Table 13a.

Table 13a. Test for independence between plant height and susceptibility to septoria tritici blotch for crosses involving isogenic lines and Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

CROSS	DWARF (< 50 cm)			SEMIDWARF (50-90 cm)			TALL (> 90 cm)				
	<.25	.25-.50	>.50\1	<.25	.25-.50	>.50	<.25	.25-.50	>.50	N	Chi-SQUARE
CB18-77262 ($Rht_1 rht_2$) x TIBET DWARF	1	1	64	5	1	60	15	8	30	185	39.247**
CB22-77267 ($rht_1 Rht_2$) x TIBET DWARF	3	15	61	20	21	32	12	5	4	173	41.455**
CB11-77253 ($Rht_1 Rht_2$) TIBET DWARF	3	7	74	18	13	47	8	1	4	175	36.617**
CB23-77268 ($rht_1 rht_2$) x TIBET DWARF	2	2	50	19	15	41	34	10	7	180	71.709**
N	9	25	249	62	50	180	69	24	45	713	
Chi-SQUARE	17.493**			52.975**			26.023**				

\1 : (SPC) = Septoria Progress Coefficient = Disease height (cm)/Plant height (cm).

** : Highly significant (Probability P = < 0.0001)

Chi-square values were high for all comparisons within classes and within crosses. Therefore the null hypothesis for independence between plant height and susceptibility is rejected with a clear tendency for short stature plants and susceptibility to septoria tritici blotch to be associated.

Based in the frequency distribution of the F_2 generation for heading date presented in Appendix Figures 5 through 8 three classes were determined: a) early < 129 days, b) intermediate 130-143 days, and c) late > than 143 days. Within each heading date class three levels of resistance were categorized: a) resistant SPC < 0.25, b) moderately resistant SPC = 0.25-0.50, and c) susceptible SPC > 0.50. The data obtained to test the association between septoria tritici blotch within different heading date classes and Chi-square values are presented in Table 13b.

Chi-square values were significant within classes, however when the four crosses where compared no significant differences were found. The F_2 population between Rht_1rht_2 x Tibet Dwarf showed the lowest chi-square value (X^2 = 2.41) with df= 4 and Probability = .661. The F_2 between Rht_1Rht_2 x Tibet Dwarf showed the highest (X^2 = 7.50) with df=4, and Probability = .112. The F_2 between rht_1rht_2 x Tibet Dwarf constantly showed a higher frequency of resistant plants within each class, while the F_2 between Rht_1rht_2 x Tibet Dwarf showed a lower number of resistant plants. The F_2's between rht_1rht_2, and Rht_1Rht_2 x Tibet Dwarf showed similar response, although, the tendency to recover early and resistant plants was greater for the F_2 between rht_1Rht_2 x Tibet Dwarf.

Table 13b. Test for independence between heading date and susceptibility to Septoria tritici blotch for crosses involving isogenic lines and Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

CROSS	EARLY (< 129 DAYS)			INTERMEDIATE (130-143 DAYS)			LATE > 143 DAYS				
	<.25	.25-.50	>.50\1	<.25	.25-.50	>.50	<.25	.25-.50	>.50	N	Chi-SQUARE
CB18-77262 ($Rht_1 rht_2$) x TIBET DWARF	5	3	35	15	6	94	1	2	25	186	2.408 P = 0.661
CB22-77267 ($rht_1 Rht_2$) x TIBET DWARF	8	10	15	24	20	66	3	11	17	174	7.317 P = 0.120
CB11-77253 ($Rht_1 Rht_2$) x TIBET DWARF	4	6	18	17	8	86	7	8	25	179	7.493 P = 0.112
CB23-77268 ($rht_1 rht_2$) x TIBET DWARF	15	11	23	33	13	60	8	6	17	186	3.217 P = 0.522
N	32	30	91	89	47	306	19	27	84	725	
Chi-SQUARE	16.380**			34.391**			15.096**				

\1 : (SPC) = Septoria Progress Coefficient = Disease height (cm)/Plant height (cm).

** : Highly significant (Probability P = < 0.0001)

B).- PHENOTYPIC AND GENETIC CORRELATIONS

To determine whether the associations between the factors related to septoria tritici blotch were of the same magnitude for all four F_1 and F_2 populations, phenotypic and genetic correlation coefficients were computed (Table 14). In general there was close agreement in the magnitude and sign of the values among the four populations for each of the factors. High positive phenotypic values were obtained between percent coverage of disease (PCD) and septoria progress coefficient (SPC). A tendency was also found for PCD to be negatively associated with heading date. High negative associations were found between PCD, plant height, and maturity date. Septoria progress coefficient was negatively associated with plant height and maturity date. Plant height showed a negative association with heading date and positive with maturity date in both F_1 and F_2. Heading date was positively associated with maturity date in both F_1 and F_2 generations.

To measure how much of the association determined through phenotypic correlation is heritable, genetic correlation coefficients were also calculated. There was close agreement between the genetic and phenotypic correlation coefficients for the F_2 generation. Percent coverage of disease was positively associated with SPC in both F_1's and F_2's. The close association between these two traits was clearly manifested in both phenotypic and genetic correlations. Percent coverage of disease was also negatively associated with maturity date and plant height. A discrepancy exists when determining the genetic association between PCD and SPC with heading date.

TABLE 14. Phenotypic and genetic correlation coefficients among percent coverage of disease (PCD), septoria progress coefficient (SPC), plant height, heading and maturity date for F_1 and F_2 generations for crosses involving isogenic lines and Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

CROSS	CHARACTERS	PHENOTYPIC CORRELATIONS F_1	N	F_2	N	GENETIC CORRELATIONS
CB23-77268	(PCD) vs					
(rht_1rht_2)	(SPC)	0.977**	19	0.949**	180	0.946
	Plant height	-0.268	19	-0.606**	180	-0.654
	Heading date	-0.351	19	0.036	180	0.375
	Maturity date	-0.731**	19	-0.241**	180	-0.216
	(SPC) vs					
	Plant height	-0.328	19	-0.646**	180	-0.672
	Heading date	-0.331	19	0.089	180	0.359
	Maturity date	-0.765**	19	-0.219**	180	-0.187
	Plant height vs					
	Heading date	-0.025	19	-0.298**	180	-0.296
	Maturity date	0.459*	19	0.025	180	0.019
	Heading date vs					
	Maturity date	0.602**	19	0.677**	180	0.490
CB22-77267	(PCD) vs					
(rht_1Rht_2)	(SPC)	0.902**	8	0.968**	173	1.037
	Plant height	0.166	8	-0.570**	173	-0.675
	Heading date	0.048	8	0.100	173	0.110
	Maturity date	-0.431	8	-0.232**	173	-0.232
	(SPC) vs					
	Plant height	-0.214	8	-0.519**	173	-0.533
	Heading date	0.355	8	0.073	173	0.056
	Maturity date	-0.082	8	-0.263**	173	-0.260
	Plant height vs					
	Heading date	-0.949*	8	-0.307**	173	-0.304
	Maturity date	-0.764*	8	0.009	173	0.033
	Heading date vs					
	Maturity date	0.564**	8	0.798**	173	0.807

**, * = Significantly different at the 0.05 and 0.01 level.

Table 14. continued

CROSS	CHARACTERS	PHENOTYPIC CORRELATIONS F_1	N	F_2	N	GENETIC CORRELATIONS
CB18-77262	(PCD) vs					
(Rht_1rht_2)	(SPC)	0.301*	38	0.945**	185	1.246
	Plant height	-0.098	38	-0.614**	185	-0.357
	Heading date	0.066	38	0.065	185	0.089
	Maturity date	0.207	38	-0.213**	185	-0.286
	(SPC) vs					
	Plant height	-0.251	38	-0.533**	185	-0.534
	Heading date	0.033	38	0.019	185	-0.183
	Maturity date	-0.324*	38	-0.194*	185	-0.476
	Plant height vs					
	Heading date	0.337*	38	-0.429**	185	-0.255
	Maturity date	0.380*	38	-0.124	185	-0.069
	Heading date vs					
	Maturity date	0.566**	38	0.815**	185	0.799
CB11-77253	(PCD) vs					
(Rht_1Rht_2)	(SPC)	0.267	19	0.950**	175	0.948
	Plant height	-0.261	19	-0.517**	175	-0.543
	Heading date	0.226	19	-0.162	175	0.078
	Maturity date	-0.379	19	-0.415**	175	-0.233
	(SPC) vs					
	Plant height	0.373	19	-0.456**	175	-0.596
	Heading date	-0.373	19	-0.174*	175	-0.002
	Maturity date	-0.142	19	-0.430**	175	-0.003
	Plant height vs					
	Heading date	0.460*	19	-0.249**	175	-0.219
	Maturity date	0.503*	19	-0.058	175	-0.082
	Heading date vs					
	Maturity date	0.366	19	0.793**	175	0.265

**, * = Significantly different at the 0.05 and 0.01 level.

The positive genetic correlation coefficient between these traits might indicate that plants which headed earlier were more resistant than late heading plants. However, this association was only slightly significant for the cross between rth_1rht_2 x Tibet Dwarf. The genetic correlation coefficients between plant height and heading and maturity date were negative for all crosses, except for the cross between rht_1Rht_2 x Tibet Dwarf. In this cross a positive genetic association was found between plant height and maturity date. This suggests a tendency for tall plants to be associated with late heading and late maturity. A high positive genetic correlation coefficient was constantly found between heading and maturity date in the four crosses.

DISCUSSION

This study was designed to address the question as to whether there is a differential response of the Norin 10 height reducing genes (Rht_1 or Rht_2) to the severity of septoria tritici blotch. To provide a common genetic background, four isogenic lines were used. These lines resulted from the backcross population 'Itana'/3/'Norin 10'/'Brevor 14'//6*'Itana. These isogenic lines were crossed to a susceptible, short, and early maturing cultivar designated as Tibet Dwarf. Resulting F_1 and F_2 generations along with the parental lines were used as the experimental material. Thus, an opportunity to determine possible associations between dwarfing sources, heading and maturity date, and reaction to septoria tritici blotch was possible. Results of this study must be interpreted in light of the genotypes used and the environment under which the experiment was conducted.

BREEDING FOR SEPTORIA TRITICI BLOTCH RESISTANCE

Establishing appropriate breeding objectives is essential for the success of all plant breeding programs. Early maturing wheat cultivars are important in a multiple cropping system and in low rainfall regions to escape drought and other abiotic and biotic stresses. Under irrigated or higher rainfall conditions higher fertility rates can be employed with short, stiff straw cultivars, thereby increasing yield levels by avoiding lodging which frequently occurs with taller cultivars.

Concerns are being expressed that the widespread use of semidwarf wheats from certain dwarfing sources may lead to greater susceptibility to diseases such as septoria tritici blotch.

Qualitative inherited traits such as plant height and heading date are easily modified in early generations. Traits which are controlled by only one or two genes can easily be recognized in early segregating populations thus allowing breeders to select effectively for such traits. However, for traits such as resistance to disease other factors have to be considered in determining the nature of inheritance and possible associations as three factors must be present to cause the disease. These include a susceptible host, a pathogen and a favorable environment.

Differences between parents, F_1, and F_2 populations in Septoria severity measured as the percent coverage of disease (PCD), and septoria progress coefficient (SPC) were observed confirming that genetic differences do exist for response to septoria tritici blotch between the Norin 10 Rht_1 and Rht_2. Thus, to select short, early maturing cultivars with acceptable levels of resistance, it will be important to select the most resistant dwarfing source when selecting parental material.

By looking at the mean values, and the orthogonal mean analysis tables presented in the results section it can be observed that the Rht_2 gene was associated with greater levels of resistance than Rht_1 gene. This higher level of resistance associated with Rht_2 was also transmitted to the F_1 and F_2 generations when combined with Tibet Dwarf. Therefore, these results indicated that improvements would appear possible for septoria tritici blotch resistance via crosses with the

Rht_2 gene which consistently was associated with the lower Septoria severity values. This might confirm results of previous reports where the Rht_2 gene was found to be associated with higher levels of resistance to both S. tritici and S. nodorum (Scott et al. 1985).

When the F_1 generation means were compared with their parents and midparent values all four F_1 populations were intermediate between the resistant and susceptible parent. Partial dominance toward resistance was observed for the F_1's with the Rht_2 allele. While the F_1 Rht_1 x Tibet Dwarf mean value was similar to the respective midparent values. This further suggests that short, resistant plants would be harder to obtain if the Rht_1 gene is used in breeding for resistance to septoria tritici blotch. However, even though the breeder of self pollinated crops can not fix genes which function in a non additive manner there appears to be considerable additive gene action involved as well with this source of dwarfness. This conclusion is supported by the fact that transgressive segregation for resistance was observed in the F_2 populations where Rht_2 was involved.

The analysis of the F_2 generation supports the information provided by the F_1 regarding resistance to septoria tritici blotch. One or two genes were found to govern resistance. This suggests that plants with acceptable levels of resistance to septoria tritici blotch can be easily achieved through early generation selection. This opportunity is further confirmed by the high heritability estimates obtained, suggesting that selection for septoria tritici blotch resistance in the F_2 generation would be effective and transmissible to later generations.

Short plant stature and earlier heading date were also partially dominant in the F_1's when compared to taller plants which had a later heading date. The high frequency of plants exhibiting early maturity and short stature in contrast to late maturity and tall plants is considered due to the partial dominant effects of Tibet Dwarf for short height and early heading.

The inheritance pattern for plant height and heading date in the F_2's generally gave similar responses for these two traits. Few genes with additive effects appeared to determine plant height and heading date. The heritability estimates were high suggesting that breeding for early heading and short stature could be achieved in early generations. However, it should be kept in mind that when selecting for short stature and earliness it is possible to increase the level of septoria tritici blotch infection.

ASSOCIATION OF RESISTANCE TO SEPTORIA TRITICI BLOTCH, PLANT HEIGHT, AND MATURITY DATE

Early maturing wheat cultivars have been associated with lower yields due to the short growing season and rapid development of foliar disease. The development of septoria tritici blotch is promoted by cooler temperatures, frequent rains, and high relative humidity from seedling to heading stage (Eyal et al 1974). These conditions were present at Corvallis, Oregon during the duration of this study (Appendix Table 4). It appears possible that greater epidemics due to septoria tritici blotch are possible if susceptible cultivars are associated with early heading and maturity dates, especially under favorable conditions for the development of the disease.

In this study shorter stature plants generally had a higher PCD and SPC which might be an indication of the ladder effect in which the inoculum reaches the upper canopy in a shorter period of time. Nevertheless, tall susceptible, and short resistant plants were recovered in the F_2 populations. In crosses where the Rht_2 dwarf gene was present a higher frequency of short stature resistant plants were recovered when compared to those populations where Rht_1 was involved.

The phenotypic and genetic correlations showed that late maturity was associated with taller plants, lower PCD and SPC. However, the evidence is not clear as to the association between early heading and susceptibility as the phenotypic and genetic correlations were low and often of different signs. Even though the heading periods were divided in three classes to elucidate the association between these two factors the test for independence was inconsistent. This might suggest that the longer the plants are exposed to the infection periods, the greater the chance of being attacked by the pathogen.

The high negative phenotypic and genetic correlation coefficients found between septoria tritici blotch and short stature in the F_2 generations suggest that these traits are associated and genetic linkage may be involved. The presence of dwarf and semidwarf resistant wheats observed in the F_2 population favors linkages rather than pleiotropism, as previous reports have suggested (Eyal et al. 1982).

In summary, the data in this study indicate that additive genetic effects were present; however, in certain crosses, the F_1 means were higher than that of the more susceptible parent. The tendency of the Rht_2 dwarf gene to be associated with resistance is of particular value in breeding for resistance to septoria tritici blotch. If Rht_2 gene is used as a source of dwarfness it must be combined with other sources of resistance to achieve acceptable levels of resistance and still maintain the semidwarf stature.

Some discrepancies were noted in the results in estimating the association between septoria tritici blotch, and heading and maturity date. Negative phenotypic and genetic correlation coefficients between septoria tritici blotch, and maturity date were evident. However, when comparing septoria tritici blotch and heading date, the phenotypic and genetic correlations were low and sometimes positive although not statistically different.

Heading date and maturity date were highly correlated, and therefore can both be used to predict earliness. As far as field selection is concerned, heading date is easier to identify than maturity date.

Results of this study suggest that under the conditions which existed at Hyslop Agronomy Farm during the 1985-1986 growing season it would be possible to select shorter, earlier maturing wheat cultivars with acceptable levels of resistance to septoria tritici blotch. It would be important that the emphasis be placed on the Rht_2 dwarf gene source and that large F_2 populations must be grown to obtain the desired plant types by avoiding possible linkages between short stature, earliness and septoria tritici blotch susceptibility.

SUMMARY AND CONCLUSIONS

The main objective of this study was: 1) to determine if there is a possible association between the Norin 10 Rht_1 and Rht_2 dwarfing genes, heading and maturity date, and the severity and development of the septoria tritici blotch.

A completely randomized split plot design with three replications was used. Crosses involving isogenic lines possessing the Norin 10 height reducing genes and the Tibet Dwarf were used as a main plot. Parents and resulting F_1's and F_2's were used as subplots. Data were collected on an individual plant basis for five factors.

Characters measured were subject to analysis of variance, t-test and orthogonal contrast mean analysis to determine whether differences exist among different dwarfing genes. Phenotypic and genetic correlation coefficients and tests of independence using chi-square tests were also computed. In addition the number of segregating genes in the F_2 generation, gene action, and heritability estimates were also obtained.

The results and conclusions from this study are summarized as follows:

1. Genetic differences among cultivars were found for septoria tritici blotch severity as measured by the percent coverage of disease (PCD), septoria progress coefficient (SPC), plant height, time of heading, and physiological maturity.
2. Low coefficients of variation were observed for heading and maturity date. Values were intermediate for percent coverage of disease (PCD), and plant height. Septoria progress

coefficient (SPC), exhibited the highest coefficient of variation.

3. The Tibet Dwarf cultivar was the shortest, earliest heading, and had the highest PCD, and SPC. Among the isogenic lines only slight differences were found for heading date. However, significant differences were found for PCD, SPC and plant height.

4. When comparing the two semidwarf isogenic lines, Rht_1 and Rht_2 the latter had the lowest PCD and SPC.

5. Analysis of the F_1 generation showed that there was a general tendency from partial to no dominance for PCD, plant height, and heading date.

6. Among the F_1's, Rht_2 x Tibet Dwarf had the lowest PCD and the latest heading date with the Rht_1 x Tibet Dwarf cross having the highest PCD values. Crosses between Rht_1Rht_2 x Tibet Dwarf gave the shorter F_1 population with rht_1rht_2 x Tibet Dwarf being the tallest.

7. The F_2 analysis suggested that additive type of gene action is present in determining resistance to septoria tritici blotch in crosses between Rht_2 and rht_1rht_2 x Tibet Dwarf. For crosses between Rht_1 x Tibet Dwarf a non additive gene action is also involved determining Septoria resistance.

8. Number of segregating genes in the F_2 generation were found to be low for Septoria severity, plant height and heading date. Broad sense heritability estimates were high for all three traits suggesting that selection for these traits will be

effective in early generations.

9. Percent coverage of disease was closely associated with SPC for both phenotypic and genetic correlations. Percent coverage of disease and SPC were associated with taller and late maturing plants as noted in both phenotypic and genetic correlations.

10. The high positive association between PCD and SPC with taller plants might suggest linkage between these traits. The presence of short resistant and tall susceptible plants in the F_2 generation support the hypothesis that linkage rather than pleiotropism is determining the association between plant height and Septoria severity.

11. No clear association between heading date, PCD and SPC were found in this experiment either through phenotypic and genetic correlations. The test for independence for these factors did not clearly support such association.

12. Short stature tended to be negatively associated with heading and maturity date. Heading date was positively correlated with maturity date.

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APPENDICES

Appendix Table 1. Observed mean square values of plant height, percent coverage of disease (PCD), septoria progress coefficient (SPC), heading and maturity date from crosses involving isogenic lines and Tibet Dwarf and resulting F_1 and F_2 populations grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

SOURCE OF VARIATION	DEGREES OF FREEDOM	PLANT HEIGHT (cm)	(PCD) (%)	(SPC)
BLOCK	2	7.231	75.911	0.072 *
CROSS	3	789.203 **	307.458 **	0.182 **
ERROR (A)	6	17.502	25.320	0.012
GENERATION	3	9733.491 **	2122.764 **	0.536 **
CROSS x GENERATION INTERACTION	9	284.526 **	81.305 **	0.054 *
ERROR (B)	24	15.766	15.680	0.007
TOTAL	48			

SOURCE OF VARIATION	DEGREES OF FREEDOM	HEADING DATE (days)	MATURITY DATE (days)
BLOCK	2	0.294	0.287
CROSS	3	1.818	11.027 **
ERROR (A)	6	3.038	2.985
GENERATION	3	1134.982 **	2758.232 **
CROSS x GENERATION INTERACTION	9	9.571	7.649
ERROR (B)	24	6.100	4.179
TOTAL	48		

*, ** = Significantly different at 0.05, and 0.01 respectively.

Appendix Table 2. Observed mean values, standard deviations and coefficients of variation of five factors from crosses involving isogenic lines and Tibet Dwarf and resulting F_1 and F_2 populations grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

VARIABLE	MEAN	STANDARD DEVIATION	COEFFICIENT OF VARIATION (%)
PLANT HEIGHT	67.4	4.0	5.9
(PCD)\1	37.4	6.1	9.7
(SPC)\2	0.6	0.1	13.1
HEADING DATE	134.4	2.5	1.2
MATURITY DATE	170.5	2.1	0.8

\1 = (PCD) = Percent coverage of disease in the uppermost four leaves.
\2 = (SPC) = Septoria progress coefficient. Disease height (cm)/plant height (cm).

Appendix Table 3 . Summary of grass clumps observed in the F_2 populations for crosses between isogenic lines and Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

CROSS	BLOCK I	BLOCK II	BLOCK III
CB11-77253 (Rht_1Rht_2) x TIBET DWARF	16\1	12	13
CB18-77262 (Rht_1rht_2) x TIBET DWARF	18	13	16
CB23-77268 (rht_1rht_2) x TIBET DWARF	13	13	17
CB22-77267 (rht_1Rht_2) x TIBET DWARF	18	16	17

\1 = Type I grass clump. (Hermsen 1967, Moore 1969, and Gale 1985). A profusion of tillers with stiff dark green leaves formed a typical "grass clump". Only become reproductive when grown under long 12 hour days at 26^{0} C.

Appendix Table 4. Summary of meterological data for Corvallis, Oregon (1985-1986).

	Average temperature, ^{0}C			Radiation Langley	Evaporation mm	Relative Humidity %
	Max.	Min.	Mean			
September	22.0	7.6	14.8	342	107.25	45.53
October	17.6	4.7	11.1	225	74.25	51.48
November	7.1	-0.2	3.4	111	------	67.66
December	4.5	-3.6	0.4	117	------	70.77
January	9.7	2.1	5.9	89	------	77.00
February	10.0	3.0	6.5	133	------	73.62
March	15.6	5.3	10.4	290	------	58.12
April	15.1	4.1	9.6	381	73.50	51.53
May	18.7	6.9	12.8	496	94.00	52.58
June	25.2	10.6	17.9	578	155.50	49.13
July	24.6	10.0	17.3	547	166.00	48.87
August	30.6	11.3	20.9	516	203.20	41.72

Note: Observations were taken from Hyslop Field Laboratory.

Appendix Table 4. Continued

	Average Precipitation				
			Number days with at least:		
	Monthly (cm)	\1 daily	0.25 cm	1.25 cm	2.50 cm
September	1.98	12	3	0	0
October	9.88	14	8	4	0
November	11.91	16	11	2	1
December	9.45	9	5	3	1
January	16.59	26	16	5	0
February	25.15	20	15	8	4
March	7.72	17	9	2	0
April	4.67	16	7	0	0
May	6.35	13	7	1	0
June	0.79	4	2	0	0
July	2.92	6	2	1	0
August	0.00	0	0	0	0

\1 = Number of days with measurable precipitation.
Note: Observations were taken from Hyslop Field Laboratory.

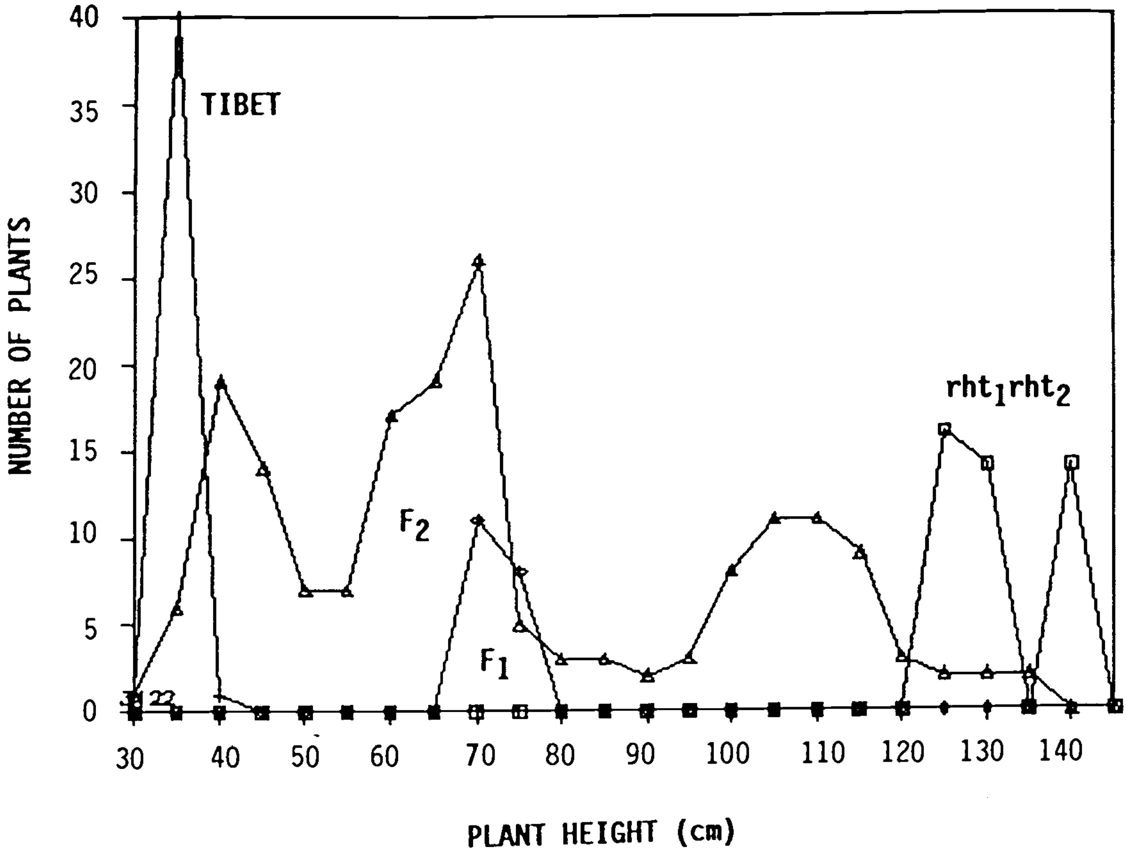

Figure 1. Frequency distribution of plant height for parents, F_1 and F_2 from cross rht_1rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

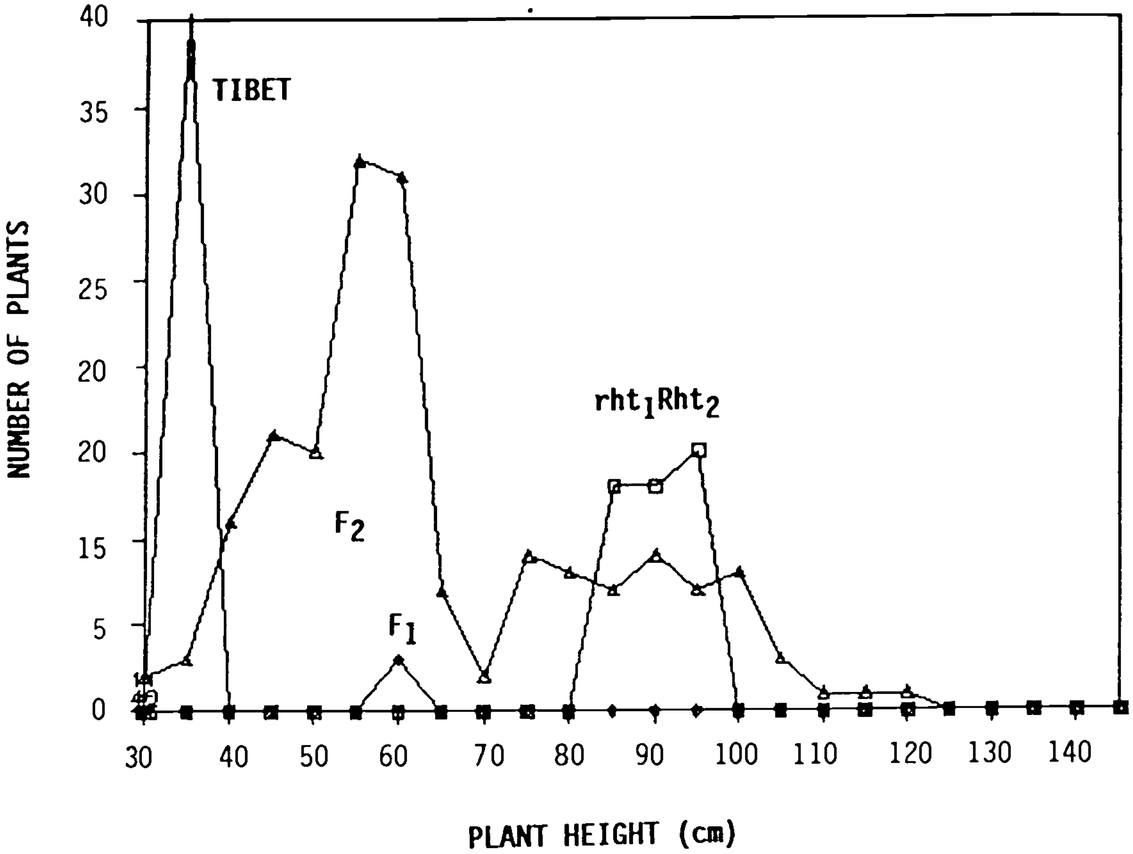

Figure 2. Frequency distribution of plant height for parents, F_1 and F_2 from cross rht_1Rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

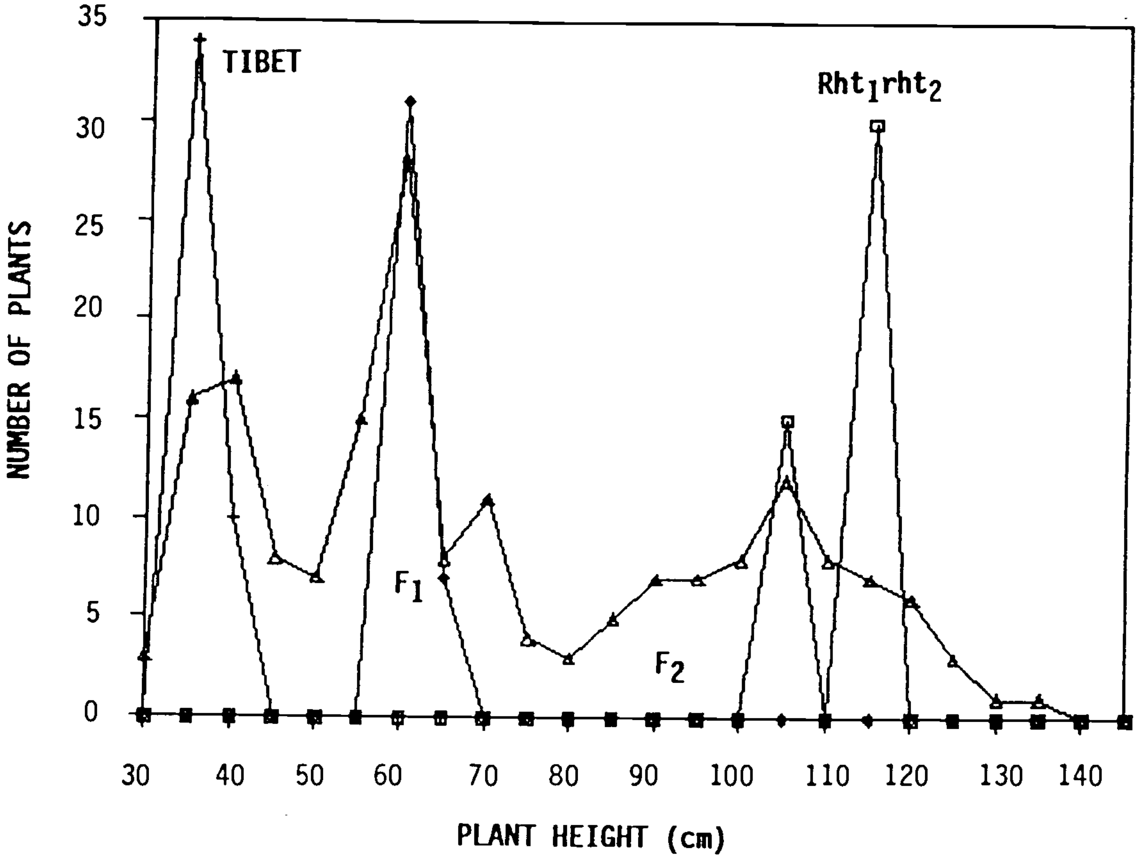

Figure 3. Frequency distribution of plant height for parents, F_1 and F_2 from cross Rht_1rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

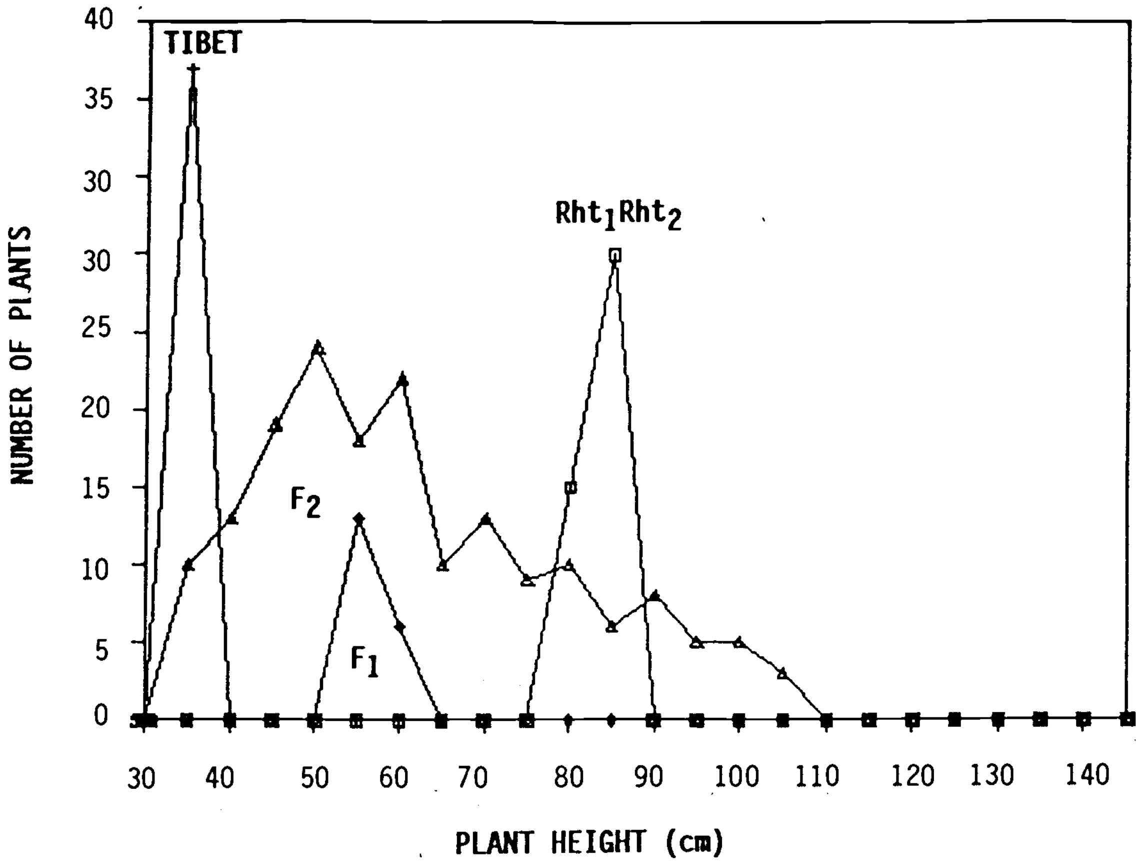

Figure 4. Frequency distribution of plant height for parents, F_1 and F_2 from cross Rht_1Rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

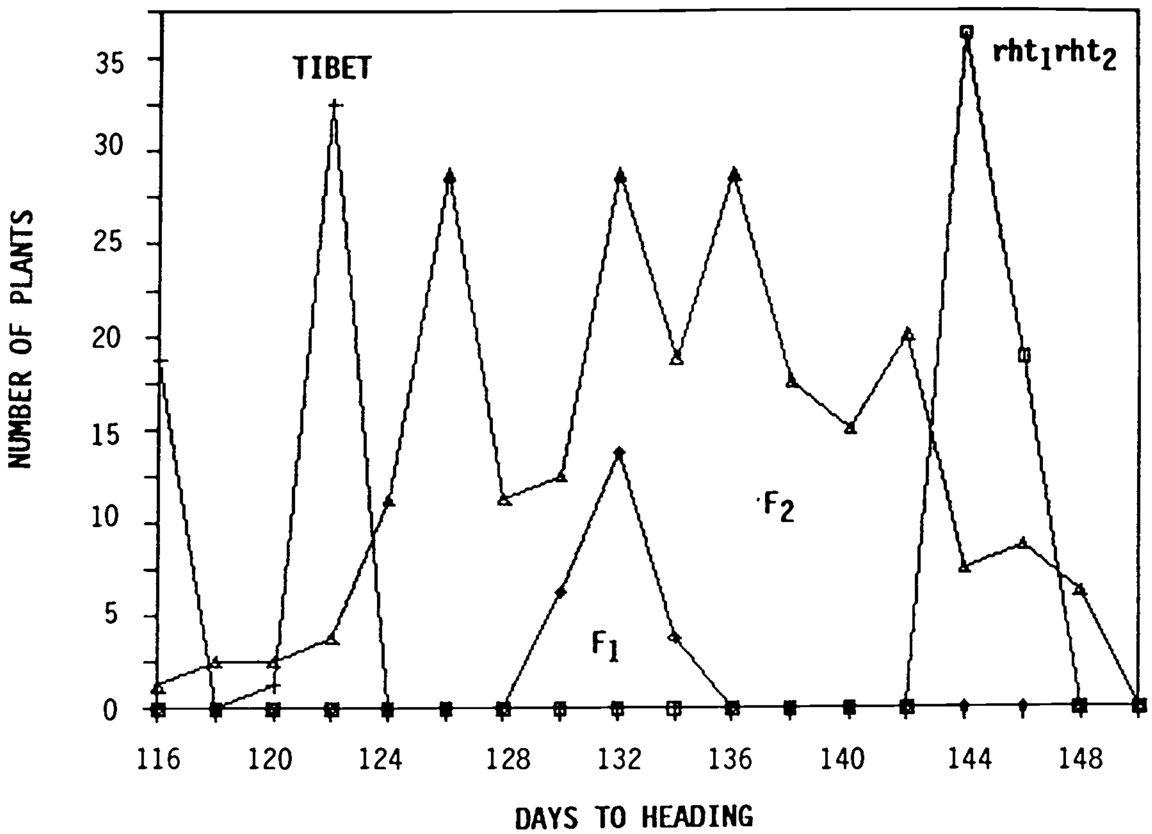

Figure 5. Frequency distribution of heading date for parents, F_1 and F_2 from cross rht_1rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

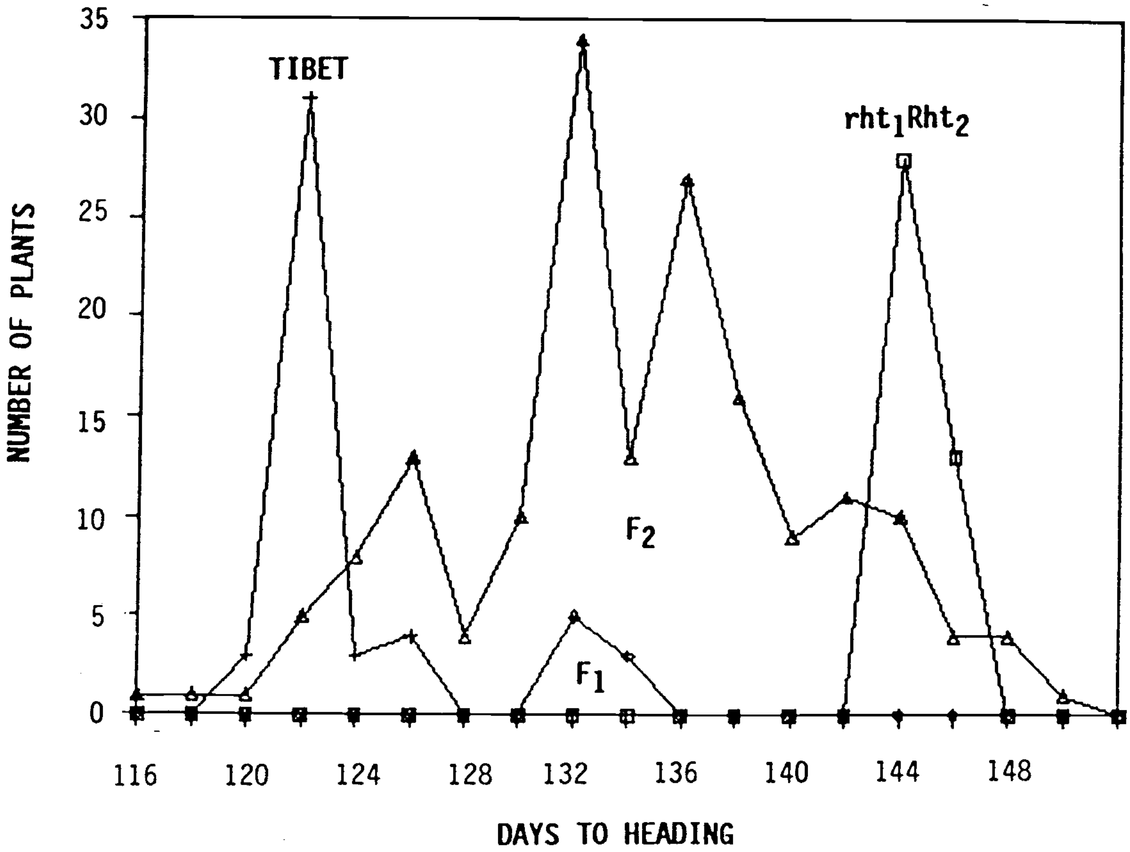

Figure 6. Frequency distribution of heading date for parents, F_1 and F_2 from cross rht_1Rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

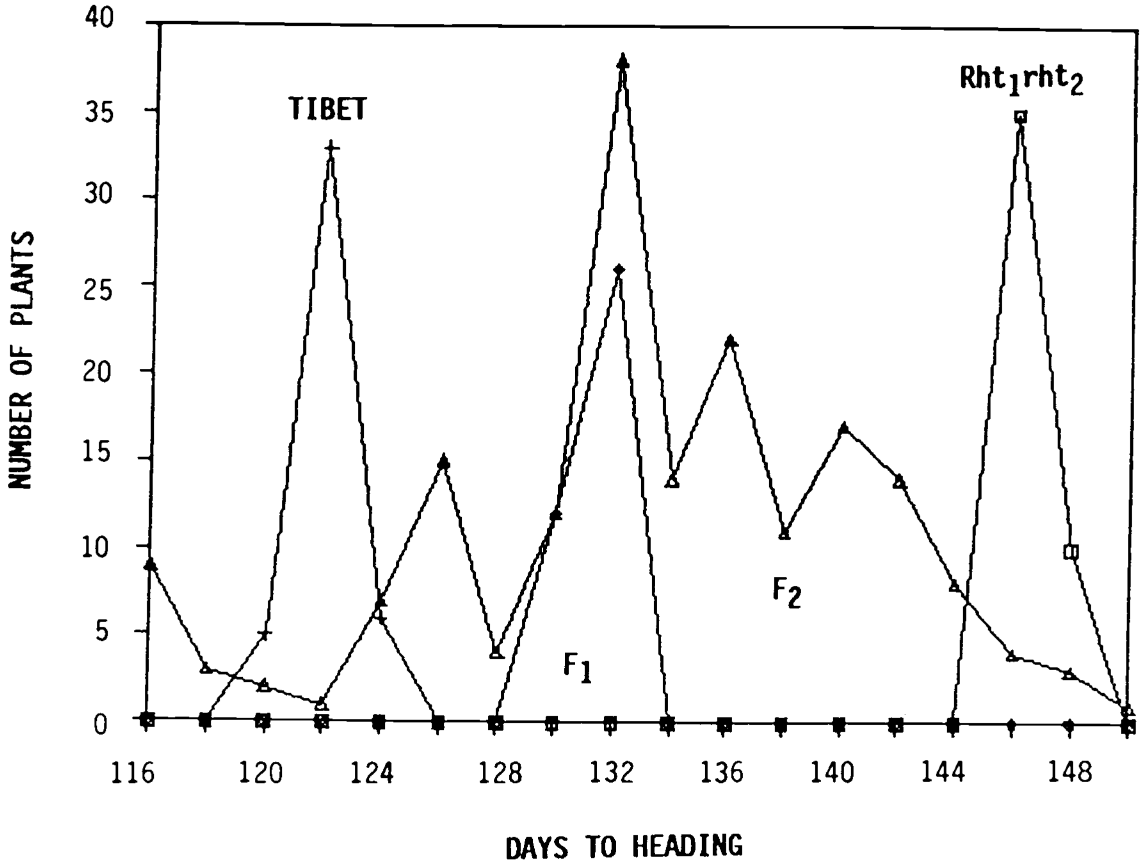

Figure 7. Frequency distribution of heading date for parents, F_1 and F_2 from cross Rht_1rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.

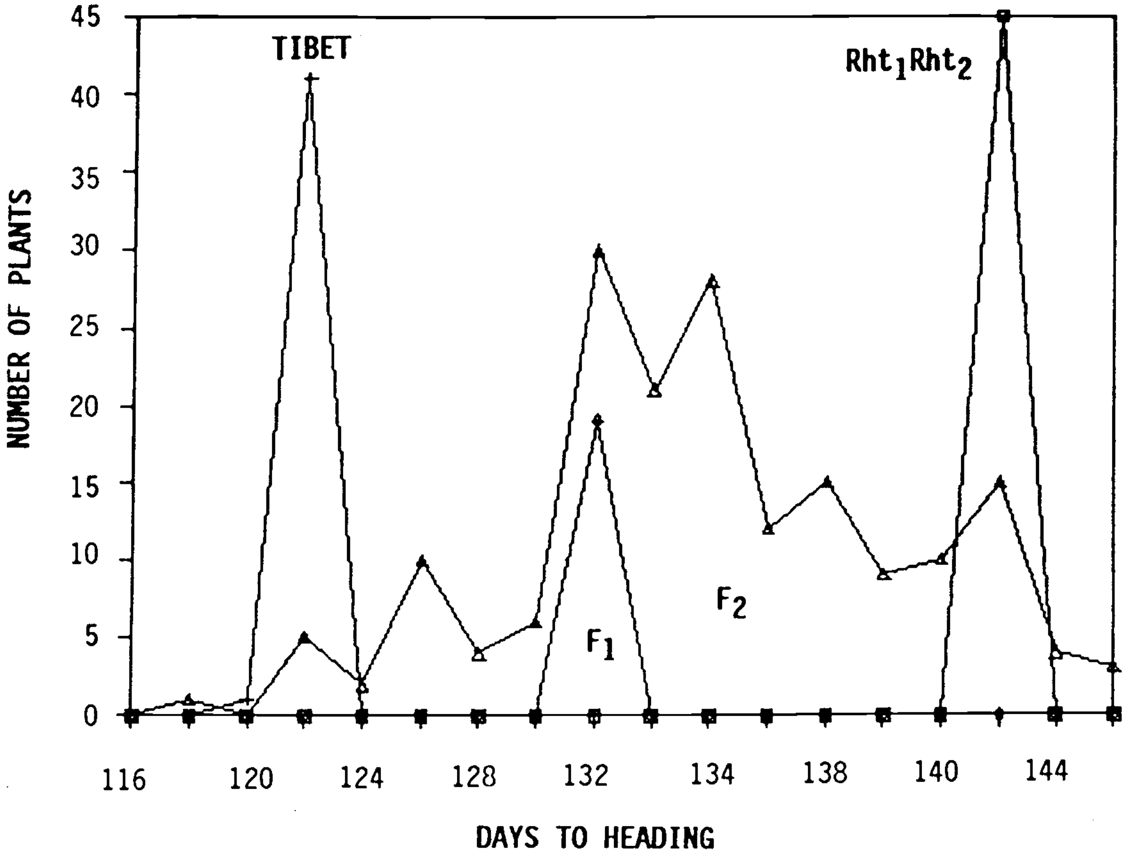

Figure 8. Frequency distribution of heading date for parents, F_1 and F_2 from cross Rht_1Rht_2 x Tibet Dwarf grown at the Hyslop Agronomy Farm. Corvallis, Oregon, 1985-1986.