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Influence of abiotic and biotic factors were examined in selected winter wheats previously identified as representing a range of responses to septoria infection. In the greenhouse two and three inoculations identified resistance when disease severity was assessed either for the top four leaves or the flag leaf respectively. Kernel number per spike and late tillering were more effected than kernel weight.

In a dry year, artificial inoculation and disease severity assessed at the top four leaves identified resistance in the field. Inoculum naturally present in the environment allowed the separation of resistant and susceptible entries during the wet year. The disease progress rate identified "late septoring" materials. Under dry conditions, late sown plots required a plastic film cover after inoculations to distinguish reaction patterns. An average plot yield loss of 20% was obtained by artificial inoculation under high rainfall conditions and no yield loss was recorded during the dry year. The number of kernels per spike, kernel weight, and test weight were also reduced in a high rainfall year. Under dry conditions the number of

kernels per spike was reduced in artificially inoculated plots. Kernels per spike was reduced in late sown plots, but kernel weight was reduced in these plots only in the wetter year. Grain hardness nor grain protein percent were affected by the disease.

Agreement was found between greenhouse and field disease severity estimation, but correlations between disease severity and yield were different. Correlations calculated in the field between seasons were also inconsistent.

Spike and stem dry weight (g/cm) and dry stem mono- and disaccharide content were reduced by Septoria infection. The dry weight of the top four leaves and the amount of mono- and disaccharides collected in flag leaf phloem exudate were not affected. These sugars were reduced by Septoria infection during three sampling dates in stem phloem exudate . The mono- and disaccharides of dry stem and of stem phloem exudate were negatively associated with flag leaf disease severity and positively associated with stem dry weight (g/cm).

Modifying Selected Factors to Classify Levels of Resistance or Tolerance in Wheat to Septoria Tritici Blotch

by

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Typed by Jose V. Re

DEDICATED TO:

my wife,

Susana

my children,

Diego and Sandra

my parents,

Antonio and Adelma

and my wife's parents,

Ricardo and Teresa

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INTRODUCTION

Identifying resistance or tolerance to biotic stresses is an objective of most plant breeding programs. Of the many organisms parasitizing wheat (*Triticum* spp.) *Mycosphaerella graminicola* (Fuckel) Schroeter, (anamorph, *Septoria tritici* Rob. ex Desm.) the causal agent of septoria tritici blotch, results in substantial annual losses in grain production on a world wide scale.

Many factors contribute to plant breeders' problems in working with the septoria tritici blotch-wheat pathosystem. Among breeders' concerns are: a) the lack of knowledge on the nature and extent of host resistance and pathogen virulence, b) the problems involved in isolating, accumulating, and managing sources of resistance and/or tolerance, and c) the scarcity of information on the relationship between this pathosystem and other pathogens affecting wheat. There are also difficulties arising in applying proper and uniform selection pressures throughout time and space. A better understanding of these factors would lead to more successful breeding strategies to incorporate resistance to septoria tritici blotch in wheat.

It was the intent of this research to evaluate management options of the septoria tritici blotch-wheat pathosystem and to study and characterize sources of disease resistance and/or tolerance to the disease.

To explore the factors affecting the pathosystem and to quantify the septoria-wheat interaction, a humid inoculation chamber was designed. This chamber was used to study the reaction of wheat lines

to increasing levels of septoria tritici blotch.

Experiments were also conducted under field conditions to provide information relevant to plant disease screening. In these experiments the effects of planting dates and modifications in inoculation methods on septoria tritici blotch progress and severity, and on yield components were investigated. Also, the extent of yield loss caused by the disease in several winter wheat genotypes grown in the Willamette Valley was determined. A further study investigated the effect of septoria tritici blotch on carbohydrate accumulation and transport on selected genotypes.

LITERATURE REVIEW

Importance of the Disease

Septoria tritici is one of the most damaging pathogenic fungus species in the higher rainfall wheat-growing areas of the Pacific Northwest. Here, the environmental conditions are appropriate for the development of septoria tritici blotch. As early as in 1920's the disease was reported in the United States in Wisconsin (Weber, 1922), California (Haskell, 1928), Kansas (Anonymous, 1929), and New York State (Haskell and Wood, 1929). From there on, outbreaks of the disease have been noted in almost all the wheat growing regions of the country, varying in importance each year according to the prevailing weather conditions.

Septoria tritici blotch is also an important foliar disease of wheat in other areas of the world. In Israel, specimens of wild emmer (*Triticum dicoccoides* Koern.) collected during 1902 in the Jerusalem area and of durum wheat (*T. durum* Desf.) collected in the Jordan Valley in 1924 (Eyal, 1981) were found to bear pycnidia of *S. tritici*. The authors concluded that the disease was already affecting "landraces" of bread (*T. aestivum* L.) and durum wheats before the appearance of modern wheat cultivars. More recently, the disease has been identified as a major constraint to wheat production in the Mediterranean basin (Saari and Wilcoxson, 1974), higher lands of East Africa (Stewart et al., 1972), western Australia (Rosielle, 1972), highlands of Central America (Schieber and Fumgalli, 1961), and South America (Antonelli, 1984). Shipton et al., (1971) provided a detailed review of the worldwide importance of septoria tritici blotch.

The relevance of this disease appears to have increased since the replacement in many wheat-growing areas of adapted, local wheat cultivars by high-yielding, early-maturing, short stature cultivars (Eyal, 1981). Saari and Wilcoxson (1974) have pointed out that the first dwarf wheat cultivars were selected in the absence of the pathogen; consequently they did not carry an acceptable level of resistance to Septoria. The modification of cultural practices introduced with the new cultivars have also influenced the expansion of the disease (Eyal et al., 1973, Shaner et al., 1975, Eyal, 1976, Rosielle and Brown, 1979). Increasing use of fertilizers and irrigation, increases in plant density, and modification of tillage practices and crop rotations appear to have played an important role in this expansion.

Septoria Tritici Blotch Severity and Crop Loss Assessment

Disease appraisal and crop loss assessment are of primary importance to breeders, researchers and extension agents involved in pest management programs. Chiarappa (1976) pointed out the importance of this subject to government policy-makers officials when legislating the use of pesticides.

The use of consistent disease appraisal methods and the establishment of the yield loss as consequence of the disease enable breeders to search for different forms of resistance. Furthermore, communication among scientists is enhanced by the use of a consistent disease assessment methodology. Also, extension agents, consultants,

and farmers, can more efficiently decide on the implementation of disease control measures by using information obtained through disease and crop loss assessment experiments. These experiments also provide information to administrators of research programs to allow for a more efficient allocation of resources to solve different constraints affecting crop production.

Septoria tritici blotch has long been recognized as a severe foliar disease of wheat. Caldwell (1976) has reported that in 1950, a fifty percent yield loss was caused by this disease in Indiana in a foundation seed field of the wheat cultivar Red Coat and in replicated trials of the cultivar Monon. The author mentioned that in 1957 the central soft red wheat-growing area of the United States (Arkansas, Missouri, Indiana, and eastward) suffered the first regionally severe epidemic. Caldwell and Narvaes (1960) in United States, compared unprotected with fungicide-protected wheat plots and found that septoria tritici blotch caused yield losses ranging from 10.5 to 27.6% for naturally infected and from 10.5 to 44.6% for artificially inoculated plots. In Australia, Shipton (1968) recorded losses of up to 29% compared with plots partially protected with fungicide. He reported that two species of *Septoria* were involved in that comparison. Brown (1978) described a method for estimating grain yield losses due to septoria tritici blotch. According to his estimations, countrywide potential yield losses in Australia, calculated for the wheat cultivar Victorian Wimmera, were of 19, 20, 4, and 0% for the years 1974 to 1977 respectively. These potential losses translated to a $70 (Australian dollars) per metric ton loss to wheat growers. Impressive yield gains

were reported by Kuiper (1978) in Australia by protecting wheat plots with fungicides. An increase of 72.5% in yield of the cultivar Robin was due to a much higher 1000 grain weight and to a 16% increase in number of kernels per head. In other experiments the author found a yield increase of 145, 77, and 42% on plots of Robin, Falcon and Teal wheat cultivars respectively when comparing unprotected with fungicide-protected plots. Sanderson (1964) reported losses of 8.8% in New Zealand; Jenkins and Morgan (1969) in Britain mentioned an increase of 35% in yield by applying a full spray program to control both, septoria tritici and nodorum blotches. They reported that the gain was mainly due to the increase in grain weight. Cooke and Jones (1971), also working in Britain, found that 1000 kernel weight was reduced from 16.2 to 18.6% in two spring wheat cultivars. They found higher losses in two winter wheats which suffered a reduction of 16.2 to 24.4% in the weight of 1000 kernels. Losses of 20% in yield were correlated to disease incidence of 50% by Eyal (1972) in Israel. Eyal and Ziv (1974) recorded yield losses of 23% and 1000 kernel weight reduction of 15% in the tall (height 110-120 cm) cultivar Lakhish 221. The cultivar Bet-Dagan 213, a dwarf selection of the same cross that produced Lakhish 221, supported a similar level of disease but had a 1000 kernel weight reduction of 16.59%. In Brazil, Metha (1976) recorded severe losses due to septoria tritici blotch during 1974 and 1975. During these years he observed reductions between 40 and 46% in grain weight and reduced grain quality in two spring wheat cultivars.

Septoria tritici blotch is an endemic foliar disease of high rainfall wheat-growing areas of the Pacific Northwest. During the past

four crop seasons severe epidemics of the disease have been observed in the Willamette Valley as consequence of favorable weather conditions. Yield loss caused by the disease in five soft-white cultivars in the Willamette Valley were estimated at 24.1% (Camacho-Casas, 1986). Although septoria tritici blotch was the most prevalent foliar disease, these plants were also affected by stripe and leaf rust.

Disease Cycle and Abiotic Parameters Affecting Septoria Tritici Blotch of Wheat

Septoria species are parasitic fungi that cause leaf and inflorescence spotting in a wide range of hosts. Small grain crops, various grasses and many nongramineous species of economical importance are susceptible to diverse species of this genus.

Wheat (*Triticum* spp.) is susceptible to three species of the fungi. *Mycosphaerella graminicola* (Fuckel) Schroeter, (anamorph, *Septoria tritici* Rob. ex Desm.), causing septoria tritici blotch. *Leptosphaeria nodorum* E. Muller, (anamorph, *Septoria nodorum* (Berk.) Berk.), inciting septoria nodorum blotch. The third species is *Leptosphaeria avenaria* Weber, f. sp. *triticea* T. Johnson (anamorph, *Septoria avenae* Frank f. sp. *tritici* T. Johnson), the causal agent of septoria avenae blotch. Other species of *Septoria* have occasionally been reported to attack wheat (Shipton et al., 1971).

Septoria tritici belongs to the Ascomycetae class. The organism can attack wheat in either of two states, an asexual or anamorphic, or a sexual or teleomorphic state. *Mycosphaerella graminicola*, which is the teleomorphic state of the fungus, fructifies producing pseudothecia

which bear characteristic two celled ascospores. This form is generally not readily observed since it appears on dead leaves of standing wheat stubble (Sanderson et al., 1985). The anamorph state of the organism is *Septoria tritici* Rob. ex Desm. This form causes the characteristic lesions on tissues during the wheat growing cycle. Straw colored areas of irregular shape are often elongated between parallel veins on leaves. These lesions are frequently speckled with dark points which are a distinguishing feature of the disease. These distinctive dark spots are fruiting bodies called pycnidia. Under the moist environmental conditions they produce a sticky exudate which contain many pycnidiospores.

A new disease cycle is initiated by primary inoculum which may be of different types according to the characteristics of each pathosystem. In the humid areas of the Pacific Northwest region of the United States the practice of leaving wheat stubble standing between cropping seasons is not widespread. Therefore, the pycnidiospores may play a more important role in starting the disease cycle. It is generally believed that wind blown, water borne, trash borne, and volunteer borne pycnidiospores are the sources of primary inoculum in this area. Very little research has been done on the importance that the sexual state might have in long range dispersal in this region. Sanderson et al. (1985) have pointed out that there is a natural tendency to relate the importance of a propagule to the frequency of sighting. He suggested that the importance of the sexual state is being underestimated.

In other regions, such as the Australian wheat belt, fields of

growing wheat coexist with fields of wheat stubble. In this cropping system and those of New Zealand and United Kingdom, the importance of ascospores in initiating the disease cycle under favorable environmental conditions has already been established (Sanderson and Hampton, 1978, Sanderson et al., 1985).

Once the first infection cycle has been established, and if the conditions are favorable, several cycles may develop within a growing season. The severity of the disease usually becomes more important with each new cycle when the uppermost leaves of the plants are colonized.

The latent period appears to be conditioned by the environment as well the host genotype. Latent periods as short as 11 to 15 days have been reported by Weber (1922). Fellows (1962) first noticed lesions and fruiting bodies 21 to 30 days after inoculation with greenhouse temperatures ranging from 7 to 22 ^{o}C. Holmes and Colhoum (1975) noted that under cool weather conditions the latent period could be extended to 60 days.

Moisture is an important factor regulating the whole infection cycle (Hilu and Bever, 1957, Hess and Shaner, 1985). Both, ascospores and pycnidiospores are dependent on water for their release and transport, although long range dispersal of ascospores may be more associated with air currents (Sanderson and Hampton, 1978). Eyal (1971) reported that 40% of the total spores within a pycnidium were exuded after initial wetting. Shaner and Finney (1976) studied the relation between weather and septoria tritici blotch epidemics and found that under the conditions of Indiana, a severe epidemic is likely

to develop if there were between 35 and 40 days of rain prior to flag leaf emergence. They concluded that moisture was important for all stages of the infection process although not enough quantification of the temperature and moisture requirements for epidemic development were available. Shaner (1976) found that information gathered from controlled environment experiments were not complete enough to develop a model to relate weather to epidemics. Coakley et al. (1985) developed a model to predict severity of septoria tritici blotch on wheat using climatic data. A prediction system was also developed in the United Kingdom using rainfall and atmospheric humidity data.

Temperature is another factor affecting the progress of the disease. Fellows (1962) reported that a temperature of 22 ^{o}C favored infection in most of the experiments he analyzed. Cordo de Balonga (1981) noted that 17 ^{o}C provided the best conditions for fungus colonization under a controlled environment. Temperatures of 27 ^{o}C or higher and lower than 7 ^{o}C have been shown to inhibit infection (Narvaez, 1957, Holmes and Colhoum, 1974). Hess and Shaner (1985) studied the relationship between temperature, moisture and development of septoria tritici blotch. They found a positive correlation between increased moisture and temperature after inoculation and disease severity. In their experiment susceptible cultivars were more affected than a resistant cultivar.

A few studies have shown that light intensity affects the infection and colonization process (Benedict, 1971, Cordo de Balonga, 1981). These studies coincide in that low light intensity in the range of 2000 to 3000 lux provides good conditions for disease development.

The association between low light intensities and cloudy weather conditions was pointed out by Shaner (1976). This author also noted that light intensity may be as important as it is moisture for the favorable development of epidemics. Light intensities in the range of 200 to 400 foot candles as well as total darkness during the incubation period were found to be not favorable for infection (Fellows, 1962).

Artificial Inoculation

Researchers engaged in detecting and evaluating levels of disease resistance among plant populations depended on a stable and adequate amount of disease. Nelson and Mackenzie (1973) pointed out that pathogen populations are widely variable in their genetic make up. Therefore, they suggested, it is important to apply selection pressures using inoculum which is representative of the range of variation present in the pathogen population.

A common practice in applying selection pressure to select for resistance to septoria tritici blotch is to spread straw harboring viable propagules of *S. tritici* around the wheat plants. Eyal et al. (1983a) have described the use of infected wheat stubble for field inoculations. Another method to apply selection pressure is to disseminate artificially grown inoculum over the wheat foliage. A number of different synthetic growing media have been devised to grow the pathogen in vitro. Weber (1922), Luthra et al., (1937), Shaner and Finney (1982), among others have used potato-malt agar (PMA) media. Other researchers have successfully grown the fungi on yeast-malt agar (YMA) (Gough, 1978, Krupinsky et al., 1972), oatmeal agar (OMA) (Weber,

1922, Cordo, 1978), and Czapek-Dox V-8 agar media (Cooke and Jones, 1970, Harrower, 1978).

Adequate environmental conditions to obtain a good development of the disease is another factor of concern among researchers. In the case of septoria tritici blotch, high air moisture after inoculation is considered of importance. Krupinsky (1976) noted that 48 to 72 hours of high humidity following inoculation is needed for infection. Eyal et al. (1983b) reported that 24 to 48 hours of humidity after inoculation is adequate for infection. Scharen (personal communication) sprinkle- irrigates the plots the afternoon prior to inoculation. After an evening inoculation the plots are covered with a transparent plastic film for two consecutive nights. Cordo de Balonga (1981) obtained good results inoculating plants in a greenhouse utilizing a 96-hour period of a relative humidity between 65 to 85%. Krupinsky and Scharen (1983) designed a high humidity chamber which was successfully used to infect plants with *S. nodorum* among other foliar pathogens. They utilized a 48-hour incubation time with a relative humidity of 99 to 100%. Holmes and Colhoun (1974) covered plants with polythene bags and introduced spaying nozzle into the bag. Plants were inoculated from all sides with the bags being left on the plants for 96 hours.

Optimum amount of spores per volume of inoculating solution has been indicated to be 10^6 ml^{-1} by Shaner and Finey (1982), Jenkins and Jones (1981), and Holmes and Colhoum (1974) among others. Some researchers have used a more concentrated solution. Gough and Merkle (1977) used 6×10^6 ml^{-1}. Shearer (1978) advises to inoculate

different cultivars with several inoculum concentrations to find out which is the optimum for each genotype. Since genotypes differ in their latency period, he proposed to increase inoculum concentration in cultivars with long latent period. In this way more lesions are produced which could compensate for the reduced number of disease cycles in a given growing season.

Genetics of Host Resistance to Septoria Tritici Blotch

Cultivar resistance has been proposed as the most promising way of controlling septoria tritici blotch (Shipton et al., 1971, Rosielle, 1972, Eyal, 1981, Danon et al., 1982). Breeding programs emphasizing increased resistance to this disease are being conducted at many institutions around the world. However, little is known of the genetics of the host-pathogen relationship (Rosielle and Brown, 1979, Danon et al., 1982, Shaner et al., 1975, Wilson, 1985). Relatively few studies has been done on the inheritance patterns of the different sources of resistance. Even less attention has been paid to the study of host tolerance to this pathogen.

One of the first reports on the inheritance of resistance was published by Mackie (1929). This author found a single recessive gene conditioning resistance in the wheat cultivar he studied. Additive action by two independently inherited genes was reported to control resistance in the cultivar Nabob (Narvaez, 1957). The same report describes the resistance of the cultivars Lerma 50 and P.14 as being controlled by a single dominant gene. A single dominant resistance gene was also reported to operate in the cultivar Bulgaria 68 (Rillo

and Caldwell, 1966). Rillo et al. (1970) noted that the resistance locus of an Agrotricum line was located on a single *Agropyron*-derived chromosome. Additive gene action was also found to condition resistance by van Ginkel (1986). A new form of resistance called "green leaf resistance" was identified by Shaner et al. (1975). Lines possessing this trait are characterized by slowing the disease progress without modifying the number of pycnidia per lesion. These cultivars were found to display a delayed senescence with the upper two leaves remaining green even under severe epidemics. Rosielle (1972) noted that some resistant, early maturing lines classified according to their low pycnidial production also displayed extensive leaf necrosis. This same symptom was noticed by Shaner and Finney (1982) in the soft red winter cultivar Caldwell and in other genotypes. The authors suggested that "green leaf resistance" was the result of a combination of gene actions, a type of transgressive segregation, since some of these cultivars were derived from susceptible parents. Rosielle and Brown (1979) studied the inheritance of resistance in the tall spring cultivar Seabreeze and concluded that it was being conditioned by at least three genes. The same researchers reported that the resistance in cultivars Veranopolis and IAS-20 was controlled by one gene with heritability estimates varying between 57 to 68%. Similar results were also found by Wilson (1985) who described several cultivars as having either single dominant, duplicate dominant, or single incomplete dominant gene actions for resistance. Danon et al. (1982) showed that relatively few genes were conditioning resistance to the *S. tritici* isolate IS 398A1 in the cultivars Bezostaya 1, Oasis, Fortaleza 1,

Colotana, Sheridan, and Titan. They also found that in the cultivars Chris Mutant and Olaf, the moderate resistance reaction seemed to be simply inherited. In a previous study (Shaner et al., 1975) the cultivar Oasis was found to posses monogenic-controlled resistance. Danon et al. (1982) proposed that the discrepancy on whether Oasis had one or several genes controlling resistance may be due to the physiologic specialization of *S. tritici*. They noted that isolates of populations of *S. tritici* from Israel were quite virulent. The authors noted that Septoria physiologic specialization may explain the response of Bezostaya 1 which is resistant to a large number of isolates from Israel but susceptible to isolates found in Australia and Oklahoma.

Physiologic specialization in populations of *S. tritici* was first reported by Eyal et al. (1973). Earlier attempts carried by Morales (1958) and Shearer (unpublished data, cited by Shipton et al., 1971) failed to demonstrate the presence of specialization. Beach (1919) and Weber (1922) carried out studies to identify specialized forms of the pathogen using as hosts species of grasses and *Triticum*. They found differential interactions by cross inoculating the same isolates to different host species. Eyal et al. (1973) tested over 600 monopycnidial cultures of *S. tritici* in a period of four growing seasons. They found a number of cultures differing in their pycnidial productivity, host range, and type of host interaction. The authors suggested that resistance to the specialized forms of the pathogen should not be expected to be permanently stable. Eyal et al. (1985) evaluated the virulence of 97 isolates of *S. tritici* collected from 22 countries and six geographical regions. They assembled a set of

differentials including tetraploid and hexaploid wheats, and triticales. They detected the presence of significant isolate x cultivar interaction which indicated specificity of pathogen action. They also speculated that the gene-for-gene relationship may be operating in this pathosystem. By using the computer program GENEALOGY the authors calculated that as many as 28 different resistance genes may have been present in the diverse genotypes they studied. The presence of a gene-for-gene relationship was challenged by van Ginkel (1986) who pointed out that if this kind of relationship is not operating the calculation of resistance genes is of no value. There exists controversy as to whether physiologic races can be distinguished in *S. tritici* populations. King et al. (1983) noted that most workers have been unable to distinguish races. The use of the term "race" when, as it seems to be the case in this pathosystem, specificity is only at the host-species and not at the within-species level was questioned by van Ginkel (1986). He mentioned that these differences in the level of disease produced by different isolates can be better described by difference in aggressiveness. Resistance to specialized forms of plant pathogens has been amply treated by Van der Plank (1968) and Day (1974).

Search for Sources of Resistance

The search for resistance to *S. tritici* is complicated by the number of factors affecting it. Besides the variation in the genetic make up of the pathogen population and the influence that the environment exerts on the *S. tritici* interaction, factors associated

with host genotypes makes it difficult to identify reliable sources of resistance. Morphological characteristics such as plant height and canopy architecture and traits related to the physiology of the plant such as maturity class, photoperiod and vernalization requirements are known to affect the visible characteristics of the pathosystem (Eyal et al., 1985). A number of authors have described an association between plant height, lateness, and resistance (Shaner et al., 1975, Eyal, 1981). Tavella (1978) calculated the correlation coefficients between septoria tritici blotch severity readings, plant height, and date of heading among a number of wheat cultivars. Correlations of -0.85 between days to heading and disease severity and of -0.67 between plant stature and disease severity manifested the extent of the negative association between these traits. Rosielle (1972) failed to recover early maturing resistant materials when late resistant lines were crossed with early-maturing susceptible genotypes. Eyal (1981) reported that in Israel spring wheat cultivars that matured in less than 100 days after emergence and were shorter than 112 cm showed almost no resistance to *S. tritici*. A study to determine the relationship between plant stature, maturity class, and susceptibility was carried by Danon et al. (1982). They found that a small negative correlation between pycnidial coverage and plant height indicated that neither pleiotropy or linkage were affecting these traits. The correlation between days to heading and disease severity was -0.30 which could indicate the presence of linkage between genes controlling these characters. The authors concluded that this correlation seemed to be too low to support the presence of pleiotropy. Rosielle (1972)

recovered short resistant plants in a segregant population derived from a cross between tall, late, resistant by short, early, susceptible parents. King et al. (1983) reached the conclusion that short-strawed cultivars are affected more severely by the disease as the result of presenting a more favorable microclimate for the development of the disease. No conclusive answer has been provided to explain the resistance displayed by late cultivars. Kohli (personal communication) suggested that an unreported "young plant resistance factor" could be operating for a longer time in late maturing cultivars. When this kind of protection disappears the environmental conditions may not remain conducive for disease development.

Effects of Septoria Tritici Blotch on the Physiology, Growth, and Development of the Wheat Plant

Symptoms are external manifestations of injury by a diseased plant. Although, many other changes that are not so obvious to the farmer or researcher are also brought about by diseases. A better understanding of the effects of the diseases on the metabolism of the host plant can provide direct benefits. Russel (1981) pointed out that some of them could be a gain in accuracy in disease loss assessment and the development of more effective disease control methods.

Wheat plants supporting high levels of septoria tritici blotch suffer a great loss of photosynthetically active tissues. Malcolm (1978) noted that this disease interferes with both photosynthesis and translocation, and that any one of these disruptions must affect yield. Ziv et al. (1981) supported the idea that loss of green leaf tissue in

plants due to septoria tritici blotch disrupts the grain-filling process. On the other hand, some researchers have found that a reduction in photosynthetic capacity by defoliation or shading does not result in very large reductions in grain weight (Jenner and Rathjen, 1972, Fisher and Hille RisLambers, 1978). King et al. (1983) pointed out that although it has not yet conclusively demonstrated, the detrimental effects of destruction of a small area of photosynthetically active tissues is expected to be compensated by augmented carbohydrate production by non-colonized green tissues. Such a compensation was demonstrated to be operating in plants infected with *S. nodorum* by Wafford and Whithebread (1978). These plants increased the number of grains on tiller with moderated infection to compensate for the yield lost in the most severely affected main tillers. Compensation was also observed by these authors (1976) in healthy leaves which increased their export of assimilates to make up for the loss that occurred in diseased leaves. According to Ziv et al. (1981) the endurance of yield components of tolerant cultivars, those that maintain stable performance under a disease condition, could be the expression of a general compensatory response mechanism. Forrer and Zadoks (1983), assuming that the flag leaf produces about one quarter of the grain-filling assimilates, calculated the yield depression due to *S. tritici* on the flag leaf as being around 900 kg ha^{-1}.

By observing apical meristems of the wheat cultivar "Maris Butler" Lim and Gaunt (1978) found that early infection affected several yield components such as total floret number, floret development, and floret death. Other cultivars also showed a reduction in the number of

florets which developed and in mature grain number. No effects were found on the number of fertile spikes per unit of area. According to the researchers, if sink limitations occur early during plant development, compensatory mechanisms of later-determined component of yield such as grain weight, may not be sufficient to make up for this loss.

Ziv and Eyal (1976) noticed that yield losses observed in lateral tillers are usually larger that those measured in the central tiller. They proposed that this effect is due to a lateness in development and shorter stature of secondary tillers, characteristics that could favor high disease severity. Nevertheless, they reported that in some environments this situation can be the reverse. Harrower (1978) found that *S. tritici* significantly reduced tillering in two of the three cultivars analyzed.

Straw weight and length was not found to be affected by *Septoria* infection (Cooke and Jones, 1971, Shipton, 1968). On the other hand Caldwell and Narvaez (1960) observed a reduction in straw length when the pathogen destroyed all the foliage after flowering.

Root production was reduced 50% in young winter wheat plants grown in a greenhouse when infected with *S. tritici* (Gough, 1976). Similar results were obtained by Gough and Merkle (1977) in three winter wheat cultivars which had root yield reductions of 31.4 to 61.1% and foliage yield reductions of 12.5 to 19.4%.

Scharen and Krupinsky (1969) measured photosynthesis in spikes and flag leaves of four wheat cultivars infected with *S. nodorum*. In all genotypes analyzed they found a reduction in photosynthesis due to the

disease, although variation was found in yield and photosynthesis reduction when comparing cultivars having equivalent levels of infection. Krupinski et al. (1973) measured a reduction in the apparent photosynthetic rate of wheat plants infected with *S. nodorum*. This reduction was more evident on spikes and peduncles than in flag leaves. Scharen et al. (1975) reported that lesions due to *S. nodorum* on flag leaf axil and sheath immediately below the axil did not prevent assimilates from being translocated out of the flag leaf. They concluded that the yield reduction observed may have resulted from causes other than a reduction in transport. One of the causes they suggested could have been an alteration in the metabolism of glucose to lipids. The authors also found that *Septoria* enhanced translocation of carbohydrates to kernel, perhaps by an early senescence of leaves. Other effects of the disease on the metabolism of the plant are a decreased ascorbic acid content and an increase in peroxidase activity (King et al., 1983).

Soluble sugars accumulate in cereal stems until shortly after anthesis (Stoy, 1979). During that time demand is low and excess carbohydrates are stored. As the kernels start developing, part of these reserves are mobilized to the spike. The contribution that these assimilates make to the final grain weight under nonstress situations has been calculated to be no more than 10-12% (Wardlaw and Porter, 1967). Other authors have reported values averaging 7% (Austin et al., 1977) and 43% (Gallagher et al., 1975). According to Jenner (1986) the assimilates produced before anthesis can exceed 25% of the total imported by grains only under stress conditions.

Changes in wheat stem weight during the grain-filling period were measured by Hunt (1978). All the cultivars measured showed an increase in stem weight up to 14-21 days after spike emergence and a reduction the subsequent 21 days. Rawson and Evans (1971) estimated that on an average 33% of the weight lost by stems could be due to respiration and the rest can be accounted for by mobilization to the spikes. Genotypes growing under unfavorable conditions for grain-filling may have an advantage if they can utilize large amounts of assimilates stored before anthesis (Gallagher et al., 1975).

MATERIALS AND METHODS

Experimental plant material used in this research was selected to represent an array of winter wheat genotypes, showing diverse response to *Septoria tritici* infection. Pedigree, Septoria reaction, and some agronomic information related to the plant material used in this research is presented in Appendix Table 1.

Field experiments were conducted at the Hyslop Agronomy Farm, located 11 km northeast of Corvallis, Oregon. There the soil type is a fine silty mixed mesic Aquultic Argixeroll. A total of 170 kg ha^{-1} per growing season of nitrogen was applied in three split applications using first urea (46-0-0), then ammonium chloride (21-0-0), and last ammonium nitrate (23-0-0). Weeds were controlled by hand hoeing and with a preemergence application of a mixture of alachlor (1.76 L ha^{-1}) and chlorsulfuron (21 g ha^{-1}). Four different studies were conducted in this research.

Inoculum Preparation

Cultures of *S. tritici*, which were used in all artificial inoculations, were obtained from wheat leaf samples collected at Hyslop Agronomy Farm during the years 1984 and 1985. Cultures were maintained in test tubes on solid yeast-malt agar medium (YMA) and transferred weekly to fresh medium. Yeast-malt agar medium was prepared using 4 g of yeast extract, 4 g of malt extract, 4 g of sucrose, and 15 g of agar per liter of distilled water. Either 0.133 g of kanamycin sulfate or 10 mg of gentamicin sulfate per liter of medium was added before autoclaving. Colonies were maintained under constant light provided by two 40-watt fluorescent tubes which were placed 80 cm above the test

tubes.

Septoria tritici was increased in liquid medium and adjusted to a concentration of 1 x 10^6-10^7 spores per ml of suspension. The liquid medium was prepared using 9 g of yeast extract, and 9 g of sucrose per 900 ml of distilled water. Kanamycin sulfate was added at a concentration of 0.133 g L^{-1} before autoclaving. Five hundred milliliters of liquid medium were placed together with approximately 1-cm^2 pieces of *S. tritici* agar-growing colonies into 1000 ml glass flasks. Liquid cultures were agitated during 5-7 days on a shaker (Burrel Wrist-Action Shaker) at 20-25 ^oC. Inoculum suspension was also prepared by harvesting *S. tritici* colonies grown on solid medium. Petri dishes were scraped with a razor blade and the collected spore masses were diluted with distilled water to achieve the desired concentration. Before applying to the plants one drop of a surfactant (Tween 20) was added per 100 ml of spore suspension.

Study 1

Effect of Septoria Tritici Blotch Severity on Wheat Grown Under a Controlled Environment.

Experimental plant material used in this study were lines 1, 6, 7, 10, 11, 12, and 13 (See Appendix Table 1). Seeds were sown on September 30, 1985 on a vermiculite medium. Containers were placed in a growth chamber and left at constant 8 ^oC for 56 days to vernalize the seedlings. The chamber was set for cycles of 12 hours of light followed by 12 hours of dark. Seedlings were irrigated with a Hoagland complete solution (Hoagland and Arnon, 1950) as needed. After the

vernalization period was completed, individual seedlings were transplanted to 15 cm pots containing a silt loam growing medium amended with 11 g of lime and 5 g of Peters fertilizer 20-20-20. Potted plants were placed on inoculation chambers constructed on a greenhouse bench. The greenhouse temperature was maintained between 18 and 21 ^{o}C. Daylength was set at 9 hours. On January 15, light duration was increased to 16 hours. Plants were fertilized twice with a total of 5 g Peters fertilizer 20-20-20 per pot.

Each inoculation chamber accommodated 35 pots and had a dimension of 90 by 120 cm by 150 cm tall. They consisted of a wooden frame lined with clear polyethylene on all sides except the bottom. A 5-cm layer of vermiculite was placed to facilitate water drainage at the bottom of each chamber. The polyethylene film of the front, back, and top of the chambers could be removed to facilitate air circulation and access to the plants between inoculations. A ultra-low-volume sprayer (Micron Co.) was connected to a water supply line and to a 6-volt battery and placed at the top of each chamber. Chambers representing a replication of a similar treatment were connected together to be turned on or off independently for each treatment.

Plants were harvested in April 10 and 11, 1986 by cutting with hand clippers near the soil surface. Plants were weighed, manually threshed, and seeds separated from the chaff with an aspirator separator. Seeds were weighted and counted with a electronic seed counter.

Three hundred ml of *S. tritici* inoculum per chamber were sprayed on plants using a battery propelled ultra-low-volume sprayer (Micron

Co.). After each inoculation, water was misted continuously for 56 hours over the plants.

The experiment was arranged as a split plot complete randomized block design in which each bench represented a block, inoculation treatments were the main plots and lines the subplots. Phenological stages at which inoculations were applied are outlined in Appendix Table 2.

Independent variables measured from each pot included:

Heading date: number of days from January 1 to emergence of the first spike.

Disease severity: disease symptoms were assessed at maturity before plants started to turn senescent. Disease severity was calculated at two different leaf levels as the percent of leaf area killed by the pathogen. The flag and top four leaves area affected by the disease was individually obtained for each plant as the average of the four or five most uniform and older tillers.

Biological yield: total weight of the plant biomass above soil level.

Tillers number

Number of spikes and grain yield per plant

Number of seeds per plant and 1000 kernel weight

Harvest index: grain yield divided by biological yield.

Values used in the analysis represented the means of five pots which were randomized within each inoculation chamber.

Study 2

Effect of Septoria Tritici Blotch on Wheat Grown Under Field Conditions.

Experimental plant material used in Study 2 consisted of lines 1 through 10 (See Appendix Table 1). The experiment was conducted over two consecutive growing seasons, 1984-1985, and 1985-1986.

Experimental lines were sown in six-row plots, 5 meters long, with 15 cm between rows. The plots were arranged in a split plot complete randomized block design with three replications. Three treatments were the main plots, and ten lines the subplots. Main plots were bordered by the cultivar Hill 81 which was planted in a manner similar to the experimental plots.

Treatments included, protected, natural presence, and artificial inoculation of the pathogen. Absence of pathogen was assured by protecting plots assigned to this treatment with fungicide. Propiconazole was sprayed on these plots at a concentration of 100 ml AI ha^{-1}. Fungicide application started at the tillering stage and continued for a total of five times at approximately every two weeks. The last application was conducted during the early grain-filling period. Natural inoculations were accomplished with *S. tritici* inoculum released by infected host tissues and debris naturally present in the environment. Plots assigned to be artificially inoculated were sprayed with a liquid suspension of *S. tritici* spores which was prepared according to specifications described in the "Inoculum Preparation" section. The suspension was sprayed using a self propelled back pack sprayer in sufficient amount to have complete

coverage of the plot. During the 1985-86 growing cycle shredded dry wheat stubble known to have been infected with *S. tritici* was distributed over the artificially inoculated plots at the tillering stage. On the second year due to the unavailability of suitable wheat stubble this practice was replaced by an early inoculation with spore suspension. After this first inoculation, and in both years, the plots were inoculated, approximately every two weeks starting at the time of stem elongation, with three additional sprays. Inoculations were performed in the late evenings or on afternoons if cloudy conditions prevailed.

The control of two other common wheat pathogens was achieved by using lines resistant to stripe rust (*Puccinia striiformis* West.) or by spraying the whole experiment with Indar (Rohm and Haas 124) at a concentration of 560 mg IA ha $^{-1}$. This fungicide has been shown to specifically control leaf rust (*Puccinia recondita* Rob. ex Desm. f. sp. *tritici*) (von Mayer et al., 1970).

Traits measured in this study included:

Grain yield per plot: seed yield was determined from four central rows. Plots were harvested using a plot combine harvester. In the 1985-86 cycle due to some plot heterogeneity as consequence of poor emergence, less than four rows were harvested for some plots.

Number of seeds per spike: ten spikes were collected from each plot and were hand threshed. Seeds were counted using an electronic seed counter.

1000 kernel weight

Grain hardness and protein percent: measured using near-infrared

reflectance spectroscopy and Udy ground wholemeal flour (0.5 mm mesh sieve).

Disease severity: disease symptoms were assessed prior to maturity before plants started to turn senescent. On the 1985-86 cycle this information was also assessed just after heading and prior to anthesis. Disease severity was calculated at two different leaf levels as the percent of leaf area killed by the pathogen. The flag and top four leaves area affected by the disease in several plants in each plot were averaged and used in the analysis.

Study 3

Effect of Planting Date and Inoculation Procedures on Field Grown Wheat

Lines 1 through 10 (See Appendix Table 1) were sown in the 1984-85 and 1985-86 growing seasons. Lines were sown in two-row plots, 1.5 m long, 30 cm between rows. The experiment was run using a split plot design with five treatments as whole plots in a complete randomized design with three replications. Entries were used as subplot treatments. Main plots were bordered by 6-row plots of the wheat cultivar Hill 81.

Treatment descriptions are presented in Appendix Table 3. Plots assigned to treatment number 1 were covered with a clear polyethylene film after each inoculation. The film was removed the following morning. Plants on these plots were sprayed with water before inoculation if they were not wet due to natural weather conditions. Inoculation were carried following the same schedule that was described

for Study 2. As noted previously, during the 1984-85 cycle, shredded wheat straw was spread over the plots that required artificial inoculations. During the cycle 1985-86, this practice was replaced with an inoculation with liquid spore suspension. Inoculum was originated and prepared according to specifications outlined in the "Inoculum Preparation" section.

Independent variables measured in this study included:

Number of seeds per spike: ten spikes were collected from each plot and were hand threshed. Seeds were counted using a electronic seed counter.

1000 kernel weight

Disease severity: disease symptoms were assessed approximately every two weeks, starting the last week of April and ending the first week of July. Disease severity was calculated at two different leaf levels as the percent of leaf area killed by the pathogen. The flag and top four leaves area affected by the disease in several plants in each plot were averaged and used in the analysis.

Plant height: average plant height measured from soil level to spike tip including awns if they were present. This information was recorded each time that disease data were collected.

Septoria height: average plant height at which disease could be identified. This information was recorded each time that disease data were collected.

Septoria progress index: septoria height divided by plant height.

Study 4

Effect of *Septoria tritici* on Some Morphologic and Physiologic Characters of Wheat.

Wheat genotypes used were lines 1, 3, 4, 5, 7, and 10 (See Appendix Table 1). Plants of these lines from plots of Study 2 in the 1985-86 cycle were used. Consequently, the same experimental design was used with the subplot levels reduced to six. To study the mono- and disaccharide content of dry stems, lines were sampled seven times during the growing season. On the first six sampling dates phloem exudate was also extracted from flag leaves and stems to study their mono- and disaccharide content. Sampling schedule was carried according to the description presented in Appendix Tables 4 and 5. At each sampling date 0.5 m of one of the outer rows of the plot was cut with a hand sickle at the ground level. Samples were tagged and carried to the laboratory for processing. Due to the limited amount of plant material that could be processed during a day, genotypes were sampled on different dates. In a given week, lines 1 and 5 were sampled on Monday, lines 3 and 4 on Wednesday, and lines 7 and 10 on Friday. Once in the laboratory five stems were chosen from each sample. Stems, spikes and flag leaves were saved for evaluation. After stem length was recorded they were cut in approximately 10 cm pieces and dried for 24 hours in an oven under vacuum (-100 KPa) at 70 ^{o}C. Vacuuming allowed for a quicker drying at a lower temperature, a condition that precluded sugar degradation. Spikes were dried in an oven under atmospheric pressure set at 90 ^{o}C during 48 hours. The diseased flag leaf area and the healthy leaf area were calculated using

a leaf area meter (Li-Cor). From each sample, two stems were chosen having a disease level representative of the sample. From these, the flag leaves were cut with a sharp razor at the juncture between the leaf blade and sheath. This material was then placed in test tubes containing an extracting solution of 1 ml of Na_2 EDTA (ethylenediaminetetraacetic acid, sodium salt) 5 mM solution adjusted to a pH 7.5 to collect phloem exudate. For the stems, pieces 20 cm long were cut starting at the base of the peduncle. Pieces were placed vertically in their natural orientation in test tubes containing the same medium as for the flag leaf. Both, stem and leaf material were maintained in the dark at 20-25 ^{o}C during the extraction period. After 1.5 hour the extracting solution was discarded. This period allowed for removal of tissue debris and contaminant solutes from broken cells. Immediately, 5 ml of the EDTA solution was placed in each tube. After a period of 4.5 hours stems and flag leaves were removed from the tubes and the solutions containing phloem exudate were stored at -20 ^{o}C until analysis. Leaf area and green leaf area were determined in these flag leaves by using a leaf area meter.

The vacuum-dried stem pieces were weighted and then ground using a laboratory mill (Thomas-Witey Model 4, 1 mm mesh) and stored in a dry room for analysis. From the stem powder, sugars were extracted according to the following procedure: 0.25 g of ground dry stem were placed in a glass centrifuge tube with 5 ml of 80% ethanol and left in a water bath for 20 minutes at 70 ^{o}C. The tubes were then centrifuged for 15 minutes at 9000 rpm at 4 ^{o}C. The supernatant fraction was collected into a small beaker and set aside. This fraction contained,

among other components, the less polar sugars. The pellet was resuspended in water and let stand for 20 minutes at 20-25 ^{o}C with occasional shaking. Tubes were then centrifuged as it was done for the first centrifugation. The supernatant obtained in the second centrifugation was placed in the same beaker containing the first fraction. The second fraction recovered the more polar sugars. The collected solution was concentrated to less than 3 ml using a rota-vator with a water bath at 50 ^{o}C. The concentrated solution was placed in a 5 ml polypropylene tube and taken to complete dryness using a speed vacuum concentrator and stored until cleaning. Before cleaning, extracts were redissolved in 4 ml of distilled water. A sample of 0.5 ml was taken from the redissolved solution and forced through a Sep pack C18 filter cartridge using nitrogen gas. Filters were washed with 3.5 ml of distilled water and the eluant was collected together with the filtered sample. This fraction was later forced through a Millipore filter (2-4 micrometers pore) using nitrogen gas. The collected eluant was taken to complete dryness under vacuum for high performance liquid chromatography (HPLC) quantification. Before quantification sugar crystals were dissolved in 1 ml glass distilled water and 20 microliters of it were injected into a HPLC (Waters Associates) apparatus. The HPLC was equipped with a automatic gradient controller, a guard column, and a Bondapak C18 (3.9 by 300 mm) column with a 5 micrometer spherical silica packing. The flow rate was adjusted to 0.60 ml per minute. This provided a clear separation between mono and disaccharides. Sugars presence were detected using a refractometer (Pharmacia). The signal was recorded in a dual pen chart

recorder (Heat-Schlumberger) and quantified by comparing it with known concentrations of sugars. To further assess the presence of these kind of sugars a sample was run in the HPLC and fractions were collected. Fractions known to contain the mono and disaccharides were analyzed using an enzymatic procedure (Boehringer Mannheim Test-Combination catalog No. 716260) designed to detect the presence of glucose, fructose, and sucrose. After aliquotes were enzymatically treated the presence of these sugars was confirmed using a ultraviolet spectrophotometer at a wavelength of 340 nm. Fractions which signaled the presence of monosaccharides in the HPLC analysis were found by the enzymatic method to contain glucose. Fractions that signaled disaccharides contained sucrose.

A 0.5 ml sample was collected from each tube containing the phloem exudates and taken to complete dryness using a speed vacuum concentrator. Sugar crystals were dissolved in 50 microliters of glass distilled water and injected in a HPLC apparatus following the procedure previously described.

In this study in addition to the traits measured in Study 2 the following variables were also measured or calculated:

Stem height: measured on excised stems from ground level to spike base.

Flag leaf area: measured using a leaf area meter (Li-Cor)

Flag leaf green area: measuring only the green portions of the leaf after diseased areas had been removed.

Dry stems mono and disaccharide content

Phloem exudate mono and disaccharide content

Amount of sugar per unit of flag leaf area: calculated by dividing

either mono-, disaccharide, or mono- plus disaccharides flag leaf phloem content by flag leaf area.

RESULTS

The results will be independently presented for each of the four studies conducted. They will be interrelated in the discussion section.

Study 1

Effect of Septoria Tritici Blotch Severity on Wheat Grown Under a Controlled Environment

This study was conducted to evaluate how different disease severity levels affected the growth and yield of selected winter wheat entries when growing under controlled environmental conditions. To achieve this goal a proper environment had to be created to assure a successful establishment of the pathogen in the host, a satisfactory host growth, and a full expression of disease symptoms. Greenhouse conditions were appropriate for normal growth and development of wheat plants. Inoculation chambers constructed on greenhouse benches provided a satisfactory environment for the pathogen to complete its cycle.

Tables 1 and 2 present disease severity levels at the flag and at the top four leaves on each entry affected by the different treatments. The number of inoculations received by plants constituted the treatments. Disease scores represent the percentage of leaf area destroyed by the disease.

Entries suffered different levels of disease severity according to the number of inoculations they received. A significant interaction was found between entry and treatment. Entries could be grouped in

Table 1. Percentage of flag leaf area destroyed by *Septoria tritici* for entries grown in a greenhouse receiving from 0 to 6 inoculations.

Entry	Number of Inoculations					Mean 1/
	6	3	2	1	0	
1	65.88	36.50	37.25	20.50	0.00	32.03
6	6.38	0.38	0.38	0.00	0.00	1.43
7	36.75	1.63	1.00	0.00	0.00	7.88
10	6.88	0.75	1.00	0.25	0.00	1.78
11	29.63	8.25	4.50	2.00	0.00	8.88
12	97.00	77.50	63.75	36.75	0.00	55.00
13	83.50	36.88	27.00	7.88	1.00	31.25
Mean 2/	46.57	23.13	19.27	9.63	0.14	

Standard errors: 1/entry, 2.28; 2/inoculation, 2.29; inoculation x entry, 5.10.

Table 2. Percentage of the area of top four leaves destroyed by *Septoria tritici* for entries grown in a greenhouse receiving from 0 to 6 inoculations.

Entry	Number of Inoculations					Mean 1/
	6	3	2	1	0	
1	79.28	54.88	46.19	33.57	0.41	42.86
6	26.97	7.63	5.13	5.03	0.06	8.96
7	61.63	24.16	13.32	12.41	0.10	22.32
10	28.63	15.01	9.66	7.35	0.03	12.13
11	52.00	32.79	21.85	17.16	0.63	24.88
12	97.88	81.19	72.44	54.60	0.78	61.38
13	89.38	52.94	37.03	26.78	0.78	41.38
Mean 2/	62.25	38.37	29.37	22.41	0.40	

Standard errors: 1/entry, 1.94; 2/inoculation, 2.86; inoculation x entry, 4.35.

three reaction classes. Entries 1, 12, and 13 were the most affected while 6 and 10 were the most resistant and entries 7 and 11 had an intermediate reaction.

The comparison of slopes obtained by regressing disease severity on number of inoculations provides an explanation for the entry by treatment interaction. Regression coefficients between disease severity and number of inoculations are presented in Table 3. Entries 1, 7, 12, and 13, which were the most susceptible, had large regression coefficients for both flag leaf and top four leaves.

Heading dates were different for each entry; however they were not affected by the level of disease. A small interaction between lines and treatments ($p=0.066$) was observed for this variable. The heading dates recorded for the seven entries are found in Appendix Table 6. The correlation between days to heading and flag leaf or top four leaves disease severity was -0.60 ($p<0.01$, $N=140$) and -0.54 ($p<0.01$, $N=140$) respectively.

Entry and treatment variability was found for the number of seeds per spike, kernel weight, number of fertile tillers per plant, and total plant grain yield. Entry by treatment interaction was observed in the number of seeds per spike and in total plant grain yield. Information on each of the yield components measured is found in Tables 4 through 7. The cultivars Stephens and Yamhill (entries 7 and 11) had the highest 1000 kernel weight of the seven entries. Stephens together with entry 10 showed the highest number of fertile tillers per plant. Entry 12 consistently had the lowest values for all yield components.

Seed and plant yield losses were gradually increased with

Table 3. Coefficients of the regression between disease severity (y) and number of inoculations (x) for entries grown in a greenhouse receiving different number of *Septoria tritici* inoculations (N=20).

Entry	Flag Leaf	Top Four Leaves
1	10.16**	11.88**
6	1.09**	4.36**
7	6.27**	10.07**
10	1.15**	4.61**
11	5.05**	8.14**
12	15.05**	13.86**
13	14.08**	14.12**

Coefficients followed by ** are significantly different from "0" at the 0.01 probability level.

Table 4. Mean number of seeds per spike for entries grown in a greenhouse receiving from 0 to 6 *Septoria tritici* inoculations.

Entry	Number of Inoculations					Mean 1/
	6	3	2	1	0	
1	25.85	29.31	33.14	34.10	34.79	31.44
6	48.76	52.89	53.06	55.27	55.34	53.06
7	35.91	45.20	48.56	48.90	49.39	45.59
10	34.24	37.19	39.11	39.43	39.45	37.88
11	32.98	35.20	34.22	35.64	36.63	34.93
12	21.63	24.76	35.12	37.18	39.37	31.61
13	31.37	39.37	41.23	42.13	43.39	39.50
Mean 2/	32.96	37.70	40.63	41.81	42.62	

Standard errors: 1/entry, 0.65; 2/inoculation, 0.60; inoculation x entry, 1.45.

Table 5. Mean 1000 kernel weight (g) recorded in entries grown in a greenhouse receiving from 0 to 6 *Septoria tritici* inoculations.

Entry	Number of Inoculations					Mean 1/
	6	3	2	1	0	
1	37.66	39.12	40.68	41.23	40.79	39.89
6	39.86	41.10	41.32	41.25	41.76	41.06
7	47.35	51.23	52.09	52.87	52.56	51.22
10	40.21	41.43	42.33	40.46	42.76	41.44
11	49.37	49.55	51.58	50.16	50.39	50.21
12	31.06	31.23	36.56	37.66	39.22	35.14
13	38.76	41.97	43.33	43.18	43.10	42.07
Mean 2/	40.61	42.23	43.98	43.83	44.37	

Standard errors: 1/entry, 0.56; 2/inoculation, 50.48; inoculation x entry, 1.25.

Table 6. Mean number of fertile tillers per plant recorded at tillering stage in entries grown in a greenhouse receiving from 0 to 6 *Septoria tritici* inoculations.

Entry	Number of Inoculations					Mean 1/
	6	3	2	1	0	
1	5.50	5.75	7.70	7.10	8.05	6.82
6	6.25	7.95	8.30	9.90	9.40	8.36
7	5.75	8.05	9.75	10.20	11.30	9.01
10	6.60	8.65	10.05	10.00	12.90	9.64
11	7.65	7.65	7.70	9.10	10.00	8.42
12	4.30	4.70	5.85	5.45	5.30	5.12
13	6.95	6.55	7.65	7.60	8.50	7.45
Mean 2/	6.14	7.04	8.14	8.48	9.35	

Standard errors: 1/entry, 0.30; 2/inoculation, 0.28; inoculation x entry, 0.68.

additional inoculations. For the number of seeds per spike, with the exception of entries 7, 12, and 13, the difference between entries was maintained more or less constant from treatment to treatment. Entries 7 and 13 suffered a sharp decline in the number of seeds per spike after receiving six inoculations, while entry 12 had an abrupt decline after the third inoculation. When all treatments are considered, the highest number of seeds per spike was observed for entry 6 followed by Stephens (entry 7). The total plant yield of entry 11 was reduced by either one or two inoculations, but it was not further affected by additional inoculations. Stephens was the highest yielding entry when receiving either none, one, two, or three inoculations, but it suffered a considerable yield reduction when receiving six inoculations. Yield reductions of entries 1, 6, 10, 12, and 13 followed a more or less constant decreasing rate as the number of inoculations were augmented.

A significant interaction between entry and treatment was also found for harvest index. Information on this variable is presented in Table 8. The highest harvest index was found in the susceptible entry 13 and the lowest in entry 10. A generalized reduction in harvest index was noted as the amount of inoculations received by plants was increased. Entries 1 and 12 were differentially affected according to the number of inoculations they received. Entry 12 had a sharp decline in harvest index after receiving three or more inoculations. Entry 1 had a similar response, although the decline was not as pronounced as for entry 12.

The effect of treatment and entry on the vegetative aerial biomass of plants was investigated. A steady decline in plant weight was

Table 7. Mean grain yield per plant (g) for entries grown in a greenhouse receiving from 0 to 6 *Septoria tritici* inoculations.

Entry	Number of Inoculations					Mean 1/
	6	3	2	1	0	
1	5.33	6.33	10.46	9.93	11.26	8.66
6	12.26	17.30	18.44	22.23	21.42	18.33
7	9.84	19.14	24.48	26.61	29.40	21.89
10	9.33	13.34	16.73	15.77	21.73	15.38
11	12.43	13.23	13.66	16.40	18.49	14.84
12	2.87	3.51	7.34	7.54	8.15	5.88
13	8.37	10.88	13.71	13.87	15.89	12.54
Mean 2/	8.63	11.96	14.97	16.05	18.05	

Standard errors: 1/entry, 0.68; 2/inoculation, 0.40; inoculation x entry, 1.53.

Table 8. Mean harvest index measured in entries grown in a greenhouse receiving from 0 to 6 *Septoria tritici* inoculations.

Entry	Number of Inoculations					Mean 1/
	6	3	2	1	0	
1	0.42	0.46	0.52	0.51	0.52	0.49
6	0.42	0.44	0.45	0.48	0.46	0.45
7	0.45	0.48	0.51	0.52	0.50	0.49
10	0.33	0.35	0.38	0.36	0.38	0.36
11	0.39	0.40	0.41	0.41	0.44	0.41
12	0.37	0.39	0.53	0.54	0.55	0.48
13	0.45	0.51	0.54	0.54	0.55	0.52
Mean 2/	0.40	0.43	0.48	0.48	0.48	

Standard errors: 1/entry, 8.59; 2/inoculation, 1.06; inoculation x entry, 1.92.

observed from noninoculated plants to plants receiving six inoculations (Table 9). Differences among entries were detected. The interaction between treatments and entries was also significant.

The extent of the yield and yield components reduction of inoculated compared with noninoculated plants is presented in Table 10. Three or more inoculations severely decreased total plant grain yield for most entries. Entry 6 was the least affected by three inoculations. One or two inoculations reduced total plant grain yield in entries 10 and 11. Six inoculations severely reduced the number of seeds and spikes per plant in all entries. One thousand kernel weight was reduced in entries 1, 7, 12, and 13 when they received the six inoculations.

Tillering data were recorded during the first week of January, one month after seedlings were moved to the greenhouse. At maturity it was observed that there was an increase in the number of tillers over that initially counted. Of particular interest was the increase in percentage of late tillers in the noninoculated plants. The percentage of late tillers produced over that initially counted for the different entries are presented in Table 11. These percentages indicated that entries developed new tillers after tillering data were recorded. The earliest entry (12) produced in the control treatment, 43% more fertile tillers than those first recorded and one of the latest maturing entries (11) produced 251% more tillers. The presence of septoria tritici blotch affected the number of late fertile tillers. Plants that received six inoculations produced only 29% more new tillers compared with 122% produced by the control plants.

Table 9. Mean weight (g) of vegetative parts of entries grown in a greenhouse receiving from 0 to 6 *Septoria tritici* inoculations.

Entry	Number of Inoculations					Mean 1/
	6	3	2	1	0	
1	7.38	7.79	9.49	9.50	10.23	8.88
6	16.57	21.57	22.32	24.18	25.80	22.09
7	12.20	20.19	24.29	24.24	29.23	22.03
10	18.86	25.48	27.15	28.16	34.64	26.86
11	19.64	20.05	19.96	23.15	23.88	21.34
12	4.93	5.65	6.56	6.49	6.74	6.07
13	10.29	10.48	11.45	11.71	13.04	11.39
Mean 2/	12.84	15.89	17.32	18.20	20.51	

Standard errors: 1/entry, 0.72; 2/inoculation, 0.73; inoculation x entry, 1.60.

Table 10. Mean yield components and yield reduction as a percentage of noninoculated plants for entries grown in a greenhouse receiving from 0 to 6 *Septoria tritici* inoculations.

Entry	Number of Inoculations							
	6	3	2	1	6	3	2	1
	Seeds per Spike				Spikes per Plant			
1	74	84	95	98	71	74	102	93
6	88	96	96	100	68	87	92	105
7	73	92	98	99	51	72	87	90
10	87	94	99	100	53	69	82	81
11	90	96	93	97	77	77	78	91
12	55	63	89	94	81	88	109	102
13	72	91	95	97	82	78	90	90
	1000 Kernel Weight (g)				Yield per Plant (g)			
1	92	96	100	101	50	58	98	92
6	95	98	99	99	58	82	87	104
7	90	97	99	101	34	64	84	89
10	94	97	99	95	44	63	81	78
11	98	98	102	100	68	72	76	88
12	80	80	93	96	36	43	94	93
13	90	97	101	100	53	71	87	87

Table 11. Number of late tillers as a percentage of tillers counted at tillering stage for entries grown in a greenhouse receiving from 0 to 6 *Septoria tritici* inoculations.

Entries	Number of Inoculations					Mean 1/
	6	3	2	1	0	
1	100	129	165	135	192	144
6	91	131	147	171	155	139
7	137	193	250	258	257	219
10	105	134	188	200	229	171
11	212	236	247	294	351	268
12	99	105	138	130	143	123
13	160	184	244	189	226	201
Mean 2/	129	159	197	197	222	

Standard errors: 1/entry, 7.73; 2/inoculation, 14.83; inoculation x entry, 17.28.

To further assess the relationship between disease severity and plant total grain yield, and yield components, correlations were calculated among these variables. These correlation coefficients are presented in Table 12.

Total plant grain yield was the variable having the highest correlation either with flag or the top four leaves disease severity. Entries 12 and 13 had higher regression coefficients between yield and disease severity when disease severity was assessed at the flag leaf rather than at the top four leaves. However, this relationship was reversed for the other entries. Entries 6 and 10, which had the lowest disease severity levels, had lower correlation coefficients than the susceptible entries 7 and 12. Significant correlations between disease severity and yield and all yield components were observed for entry 7.

Blocking seemed to have been successful in removing variation. Replications 3 and 4 had higher values for number of seeds per spike, 1000 kernel weight, grain yield per plant, plant weight, harvest index, heading date, and Septoria severity on flag and top four leaves.

Study 2

Effect of Septoria Tritici Blotch on Wheat Grown Under Field Conditions.

During the 1985-86 and 1986-87 cycles in which this experiment was performed prevailing weather conditions were different. Information on meterological data for these years are presented in Appendix Tables 7 and 8.

Excess precipitation in October and November affected planting

Table 12. Coefficients of correlation between disease severity and yield or yield components in entries grown in a greenhouse receiving from 0 to 6 *Septoria tritici* inoculations (N=20).

Entry	Seeds per spike	1000 kernel weight	Spikes per plant	Yield per plant	Harvest index
	Disease Severity in Flag Leaf				
1	-0.21	0.14	-0.56**	-0.47*	-0.13
6	-0.51*	-0.37	-0.53*	-0.61**	-0.49*
7	-0.80**	-0.65**	-0.68**	-0.73**	-0.55*
10	-0.45*	-0.24	-0.55*	-0.56**	-0.33
11	-0.47*	-0.22	-0.32	-0.46*	-0.36
12	-0.69**	-0.52*	-0.38	-0.73**	-0.60**
13	-0.65**	-0.45*	-0.58**	-0.76**	-0.56**
	Disease Severity in Top Four Leaves				
1	-0.37	-0.02	-0.60**	-0.60**	-0.26
6	-0.53*	-0.27	-0.52*	-0.61**	-0.30
7	-0.78**	-0.56**	-0.76**	-0.79**	-0.59**
10	-0.53*	-0.40	-0.58**	-0.64**	-0.42
11	-0.47*	-0.18	-0.43	-0.54*	-0.31
12	-0.64**	-0.50*	-0.31	-0.67**	-0.55*
13	-0.61**	-0.43	-0.60**	-0.74**	-0.49*

Coefficients followed by ** and * are significantly different from "0" at the 0.01 and 0.05 probability levels respectively.

operations and seedling emergence during the 1984-85 cycle. Even though plots were not lost, the reduced plant density obtained provided a suboptimal environment for septoria tritici blotch development. Also, during this growing season precipitation was less than the average with dry conditions prevailing in April and May. This may have interfered with the normal development of septoria tritici blotch. The scarcity of rains during January, April, and May created a water deficiency that adversely affected wheat yield.

During the 1985-86 growing cycle, precipitation was near average for the region, although, moisture deficiency in March and April may have also adversely affected disease development.

As consequence of these dissimilar environmental conditions many of the measured variables had different error variances each year. Thus, it was not possible to perform a combined analysis over years. Consequently, the results will be presented without placing any statistical significance as to differences between years. Many of these differences between years will be discussed in relation to the environmental conditions.

Low disease severity was observed during the 1984-85 growing cycle. Naturally inoculated plots developed low disease levels and only traces were found on the flag leaves. This condition also prevailed in the artificially inoculated plots as well. Information on septoria tritici blotch development is presented for both cycles in Tables 13 and 14 and in Figures 1 and 2. In the 1984-85 as well as in the 1985-86 growing seasons, disease severity either at the flag or at the top four leaves was different for treatments and entries. A

Table 13. Percentage of the flag leaf area destroyed by *Septoria tritici* for entries receiving different inoculation treatments in the years 1984-85 and 1985-86.

	Inoculation Treatment							
	Fungicide Protection		Natural Inoculation		Artificial Inoculation		Mean	
Entry	84-85	85-86	84-85	85-86	84-85	85-86	84-85[1]/	85-86[2]/
1	0.33	0.00	1.00	63.33	15.00	83.33	5.44	48.89
2	1.00	0.00	1.00	80.00	5.00	86.67	2.33	55.56
3	1.00	0.00	1.00	90.00	13.33	96.67	5.11	62.22
4	0.33	0.00	1.00	20.00	16.67	56.67	6.00	25.56
5	1.00	0.00	1.00	50.00	26.67	80.00	9.56	43.33
6	0.67	0.33	1.00	13.33	1.00	20.00	0.89	11.22
7	1.00	0.00	5.00	96.67	43.33	100.00	16.44	65.56
8	1.00	0.00	2.33	46.67	18.33	80.00	7.22	42.22
9	0.67	0.00	1.00	56.67	2.33	83.33	1.33	46.67
10	0.33	0.33	1.00	36.67	8.33	63.33	3.22	33.44
Mean[3]/ [4]/	0.73	0.07	1.53	55.33	15.00	75.00		

Std. errors: (84-85) [1]/entry, 1.39; [3]/treat., 1.23; entry x treat., 2.41.
(85-86) [2]/entry, 1.80; [4]/treat., 1.62; entry x treat., 3.12.

Table 14. Percentage of the top four leaves area destroyed by *Septoria tritici* for entries receiving different inoculation treatments in the years 1984-85 and 1985-86.

Entry	Inoculation Treatment						Mean	
	Fungicide Protection		Natural Inoculation		Artificial Inoculation			
	84-85	85-86	84-85	85-86	84-85	85-86	84-85[1]	85-86[2]
1	5.00	1.67	21.67	87.00	51.67	94.67	26.11	61.11
2	8.33	12.00	16.67	94.33	40.00	97.00	21.67	67.78
3	8.33	2.67	20.00	90.33	51.67	99.33	26.67	64.11
4	5.00	1.00	28.33	63.67	48.33	85.33	27.22	50.00
5	15.00	3.00	25.00	84.33	55.00	95.00	31.67	60.78
6	6.67	2.67	10.00	69.33	13.33	73.67	10.00	48.56
7	13.33	8.67	26.67	99.33	71.67	100.00	37.22	69.33
8	13.33	2.33	28.33	83.67	58.33	95.00	33.33	60.33
9	10.00	2.67	18.33	83.67	30.00	94.67	19.44	60.33
10	8.33	6.67	21.67	73.67	45.00	87.67	25.00	56.00
Mean[3/4]	9.33	4.33	21.67	82.93	46.50	92.23		

Std. errors: (84-85) 1/entry, 1.56; 3/treat., 1.25; entry x treat., 2.70.
(85-86) 2/entry, 1.30; 4/treat., 0.91; entry x treat., 2.25.

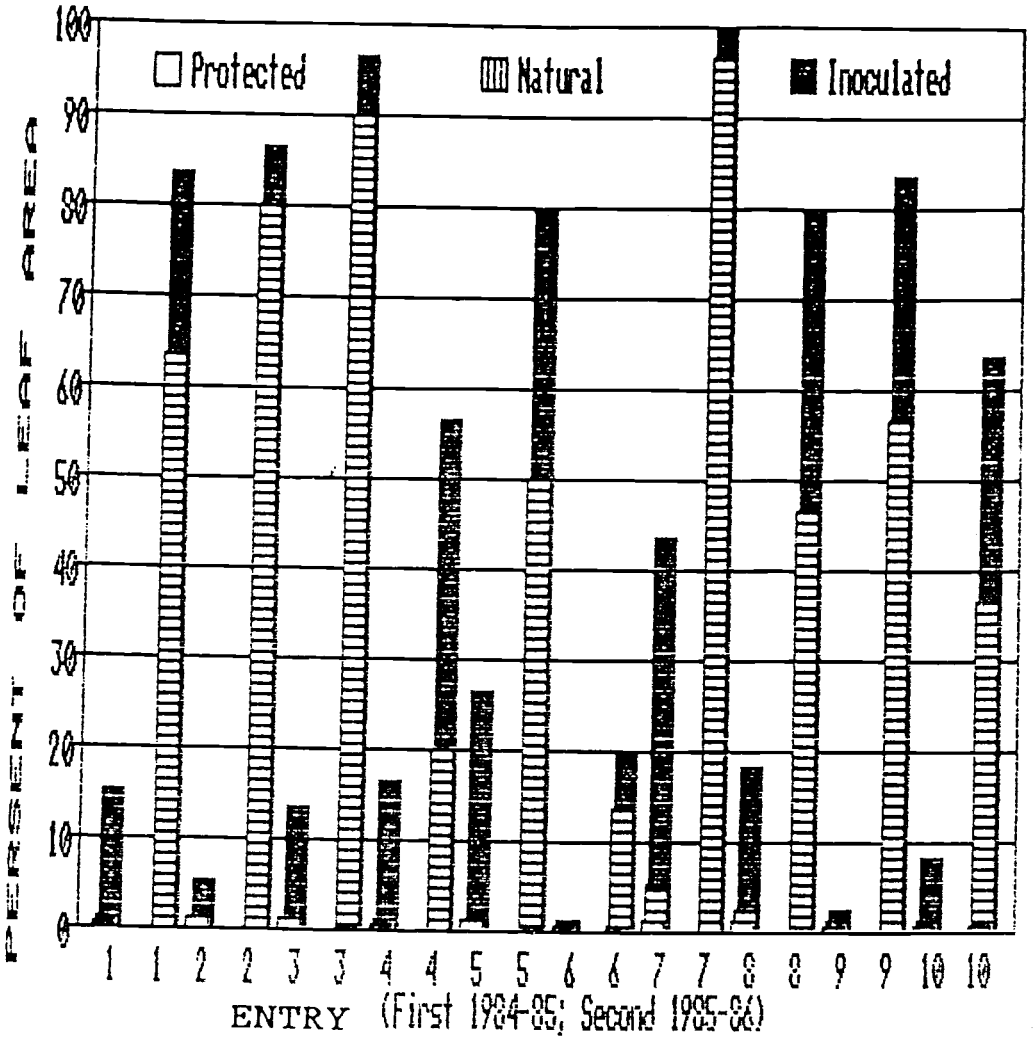

Figure 1. Percentage of flag leaf area destroyed by *Septoria tritici* in entries receiving different inoculation treatments in 1984-85 and 1985-86.

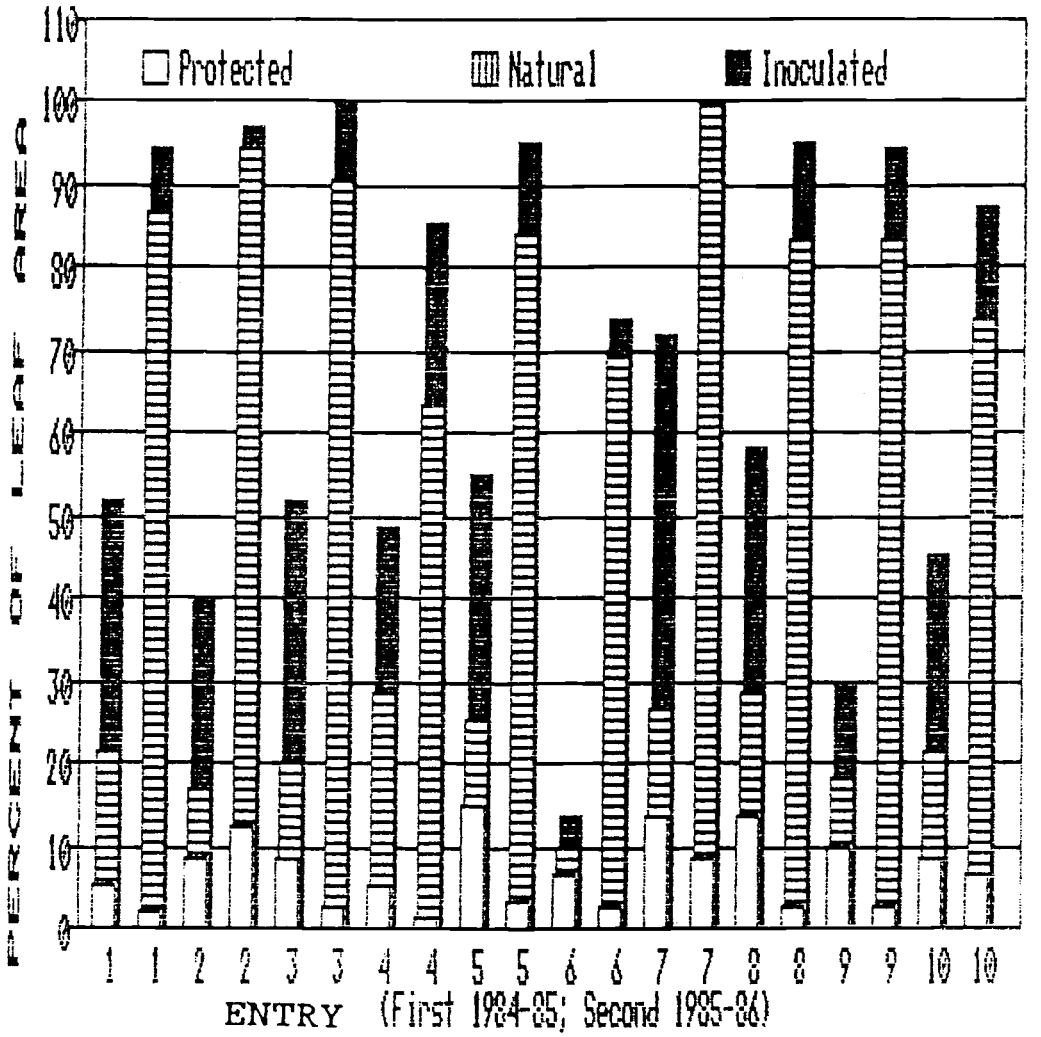

Figure 2. Percentage of top four leaves area destroyed by *Septoria tritici* in entries receiving different inoculation treatments in 1984-85 and 1985-86.

significant interaction between these two factors was also observed. This interaction was mainly due to the near elimination of disease level differences among entries when plots were protected with fungicide.

In both growing seasons, entry 6 was the most resistant and entry 7 the most susceptible. During the 1984-85 growing cycle, in naturally inoculated plots, seven entries suffered 20% or more disease severity in their top four leaves while entries 2, 6, and 9 had less than 20%. The cultivar Stephens (entry 7) had the highest values for the naturally inoculated treatment with 5% of its flag leaf area destroyed by the disease. Five entries in artificially inoculated plots had more than 50% of their top four leaves affected by septoria tritici blotch. While entries 2, 4, and 10 had between 40% and 50% with the resistant entries 6 and 9 having 13% and 30% respectively. The lowest level of disease in flag leaves in the 1984-85 cycle was found for entries 2, 6, and 9.

Artificially inoculated plots in the 1984-85 season had a twofold increase in disease at the top four leaves when compared to the naturally inoculated plots. This difference was increased to tenfold in flag leaves.

During the 1985-86 cycle a higher disease severity was recorded. In both the naturally and artificially inoculated plots, entries 4, 6, and 10 had less disease than the other entries. The most susceptible were cultivars Stephens and Malcolm (entries 7 and 3). Artificially inoculated plots had seven out of the ten entries with more than 94% of their top four leaves destroyed by the disease. The flag leaves of

cultivars Stephens and Malcolm were almost totally destroyed by the disease. Entries 4, 6, and 10 were the most resistant across treatments, and 7, 2, and 3 the most susceptible. The difference in disease severity between naturally and artificially inoculated plots was smaller than in the 1984-85 season.

The correlation between disease severity recorded in each cycle was calculated to evaluate how entries responded to a conducive and a nonconducive environment for septoria tritici blotch development. The correlations between 1984-85 and 1985-86 cycles for the top four leaves and for flag leaves disease severity were +0.72 (p=0.01) and +0.56 (p=0.01) respectively.

In Table 15 entries are ranked for both the 1984-85 and the 1985-86 cycles according to their top four leaves disease severity. Most entries maintained their ranking during both cycles. Entries 2 and 9 were resistant under a nonconducive environment, such as the one in the 1984-85 cycle, however, they became susceptible under the higher *S. tritici* pressure of the 1985-86 cycle. Entries 4 and 8 were more susceptible under low than under high *S. tritici* pressure.

For the 1985-86 growing cycle disease severity was recorded during the early and late grain filling period. Disease severity recorded at these two sampling dates are presented in Table 16. Disease progress during these two sampling periods was not the same for all entries. Some entries showed little disease progress between sampling dates. These were either resistant, such as entry 6, or highly susceptible such as the cultivars Stephens and Malcolm. Other entries such as 1 and 4, which were resistant at the first sampling date, were more

Table 15. Ranked order from low to high, according to disease severity, of entries in 1984-85 and 1985-86.

Entry	Flag leaf		Top Four leaves	
	1984-85	1985-86	1984-85	1985-86
1	6	7	5	7
2	3	8	3	9
3	5	9	6	8
4	7	2	7	2
5	9	5	8	6
6	1	1	1	1
7	10	10	10	10
8	8	4	9	4
9	2	6	2	5
10	4	3	4	3

Table 16. Septoria tritici blotch progress during two sampling dates, 6-11 and 6-28, in entries receiving different inoculation treatments in the year 1985-86.

Entry	Inoculation Treatment								
	Fungicide Protection			Natural Inoculation			Artificial Inoculation		
	6-11	6-28	Differ	6-11	6-28	Differ.	6-11	6-28	Differ.
				Flag Leaf					
1	0 1/	0	0	4	63	59	23	83	60
2	0	0	0	30	80	50	50	87	37
3	0	0	0	47	90	43	70	97	27
4	0	0	0	1	20	19	7	57	50
5	0	0	0	10	50	40	17	80	63
6	0	0	0	1	13	12	8	20	12
7	0	0	0	57	97	40	73	100	27
8	0	0	0	5	47	42	17	80	63
9	0	0	0	8	57	48	33	83	50
10	0	0	0	10	37	27	17	63	47
				Top Four Leaves					
1	0	2	1	34	87	53	55	95	39
2	12	12	0	71	94	23	82	97	15
3	2	3	1	83	90	8	91	99	8
4	0	1	1	9	64	54	26	85	59
5	2	3	1	49	84	36	66	95	29
6	1	3	1	24	69	45	46	74	28
7	8	9	1	86	99	13	94	100	6
8	1	2	1	59	84	25	74	95	21
9	3	3	0	48	84	36	70	95	24
10	6	7	0	60	74	14	65	88	23

1/ Values indicate percent of leaf area affected by septoria tritici blotch.

susceptible at the second date.

During the 1984-85 growing cycle there were differences among entries for the number of seeds per spike and for 1000 kernel weight. Protected as well as inoculated plots had the same values for these two yield components. Tables 17 and 18 present information on 1000 kernel weight and number of seeds per spike for both the 1984-85 and 1985-86 growing cycles.

During the 1985-86 season the number of seeds per spike was different among entries. Entries showed a tendency to have more seeds per spike during the 1984-85 than the 1985-86 growing cycle.

Interaction between entry and treatment was observed for the variable 1000 kernel weight during the 1985-86 growing cycle. Also, differences were found among entries and treatments. Seeds from fungicide-protected plots were heavier than seeds from inoculated plots in 1985-86. Differences between years were larger in the inoculated plots. The largest differences between years for kernel weight were observed in the susceptible cultivars Stephens and Malcolm. Kernel weight did not change for entries 1, 4, 5, and 10 in the different treatments. Much of the interaction appeared to be the effect of the more pronounced kernel weight reduction observed from protected to artificially inoculated plots for the cultivars Stephens and Malcolm. Also, the increase in kernel weight found with entries 2 and 10 from naturally to artificially inoculated plots may had contributed to the interaction mean square.

Grain yield per spike is a function of kernel weight and the number of kernels per spike. A numerical summary of the results found

Table 17. Mean 1000 kernel weight (g) from entries receiving different inoculation treatments in the years 1984-85 and 1985-86.

Entry	Inoculation Treatment: Fungicide Protection 84-85	Fungicide Protection 85-86	Natural Inoculation 84-85	Natural Inoculation 85-86	Artificial Inoculation 84-85	Artificial Inoculation 85-86	Mean 84-85 1/	Mean 85-86 2/
1	45.70	46.97	44.50	46.66	44.03	45.06	44.74C	46.23
2	48.13	48.43	49.57	43.70	46.43	45.78	48.04B	45.97
3	53.37	52.44	55.67	45.12	55.30	43.07	54.78A	46.88
4	39.07	40.69	39.67	41.39	39.47	40.22	39.40E	40.77
5	48.60	52.82	49.77	53.13	49.67	52.12	49.34B	52.69
6	50.63	46.76	49.87	43.80	49.07	43.82	49.86B	44.79
7	57.07	55.01	55.03	49.49	52.77	47.15	54.96A	50.55
8	44.40	43.27	41.50	40.57	39.87	38.74	41.92D	40.86
9	47.87	51.07	48.00	49.69	48.20	47.84	48.02B	49.53
10	53.73	48.19	54.17	48.88	52.20	50.25	53.37A	49.10
Mean 3/ 4/	48.86A	48.14	48.77A	46.24	47.70A	45.41		

Std. errors: (84-85) 1/entry, 0.64; 3/treat., 0.37; entry x treat., 1.10.
(85-86) 2/entry, 0.67; 4/treat., 0.25; entry x treat., 1.16.
Within a year means followed by the same letter are not significantly different at the 0.05 probability level (Fisher's Protected LSD).

Table 18. Mean number of seeds per spike from entries receiving different inoculation treatments in the years 1984-85 and 1985-86.

Entry	Inoculation Treatment: Fungicide Protection 84-85	Fungicide Protection 85-86	Natural Inoculation 84-85	Natural Inoculation 85-86	Artificial Inoculation 84-85	Artificial Inoculation 85-86	Mean 84-85 1/	Mean 85-86 2/
1	66.20	66.47	64.80	60.23	62.60	61.40	64.53CD	62.70CDE
2	68.27	59.27	60.73	54.50	63.73	53.57	64.24CD	55.78F
3	66.87	67.33	67.20	65.27	58.83	62.30	64.30CD	64.97CD
4	72.93	72.13	68.53	72.70	70.40	69.07	70.62ABC	71.30AB
5	67.93	62.70	67.33	56.97	65.87	59.87	67.04BCD	59.84DEF
6	79.40	68.93	78.67	66.83	70.40	63.70	76.16A	66.49BC
7	60.07	62.03	65.00	55.90	58.27	57.03	61.11DE	58.32EF
8	69.07	77.50	72.60	75.63	72.07	76.70	71.24AB	76.61A
9	69.20	54.70	64.47	38.00	65.53	52.67	66.40BCD	48.46G
10	58.73	44.47	58.27	44.17	52.53	42.43	56.51E	43.69G
Mean 3/ 4/	67.87A	63.55A	66.76A	59.02B	64.02A	59.87B		

Std. errors: (84-85) 1/entry, 1.77; 3/treat., 1.09; entry x treat., 3.07.
(85-86) 2/entry, 1.61; 4/treat., 1.01; entry x treat., 2.80.
Within a year means followed by the same letter are not significantly different at the 0.05 probability level (Fisher's Protected LSD).

for grain yield per spike is presented in Table 19. During 1984-85 spikes from protected and naturally inoculated plots yielded more grain than those of artificially inoculated plots. Differences were also found among entries resulting in a range of spike grain yield from 2.78 to 3.80 g. These differences were not reflected on a plot grain yield bases. In the 1984-85 cycle no differences were found among treatments, entries, nor the entry by treatment interaction for the variable plot grain yield. Table 20 presents information on plot grain yield for the 1984-85 and 1985-86 growing cycles.

The correlation between plot grain yield and spike grain yield during the 1984-85 growing cycle was +0.29. Only about 10% of the variation in plot yield could be explained in that season by the variation in spike grain yield. During the 1985-86 cycle, spikes from protected plots yielded more grain than spikes from inoculated plots. Spike grain yield values obtained during the 1985-86 cycle were positively correlated with plot grain yield (+0.84, $p<0.01$). In this season 71% of the variation in plot grain yield could be accounted for by spike grain yield. Differences were also found in the 1985-86 cycle for spike grain yield among entries. The lowest yielding spikes were found in entry 10 followed by entries 9 and 2. No differences were detected among the remaining seven entries. The interaction between entry and treatment for spike grain yield in the 1985-86 cycle was significant.

During the 1985-86 growing season, plot grain yield was affected by treatments. Protected plots yielded more grain than inoculated ones. Differences were also found among entries and for the

Table 19. Mean grain yield per spike (g) from entries receiving different inoculation treatments in the years 1984-85 and 1985-86.

Entry	Inoculation Treatment						Mean	
	Fungicide Protection		Natural Inoculation		Artificial Inoculation			
	84-85	85-86	84-85	85-86	84-85	85-86	84-85 1/	85-86 2/
1	3.03	3.12	2.89	2.81	2.74	2.77	2.89EF	2.90
2	3.29	2.87	3.00	2.37	2.96	2.44	3.08CDEF	2.56
3	3.57	3.52	3.74	2.94	3.25	2.68	3.52AB	3.05
4	2.85	2.93	2.72	3.01	2.77	2.78	2.78F	2.91
5	3.32	3.30	3.35	3.03	3.27	3.11	3.31BCD	3.14
6	4.02	3.22	3.92	2.93	3.45	2.79	3.80A	2.98
7	3.42	3.41	3.57	2.77	3.08	2.68	3.36BC	2.95
8	3.07	3.35	3.01	3.07	2.88	2.98	2.99DEF	3.13
9	3.31	2.78	3.09	1.88	3.16	2.51	3.19BCDE	2.39
10	3.16	2.14	3.16	2.16	2.75	2.14	3.02CDEF	2.15
Mean 3/ 4/	3.30A	3.06	3.25A	2.70	3.03B	2.69		

Std. errors: (84-85) 1/entry, 0.09; 3/treat., 0.04;
entry x treat., 0.16.
(85-86) 2/entry, 0.08; 4/treat., 0.04;
entry x treat., 0.13.

Within a year means followed by the same letter are not significantly different at the 0.05 probability level (Fisher's Protected LSD).

Table 20. Mean plot grain yield (kg/ha) from entries receiving different inoculation treatments in the years 1984-85 and 1985-86.

Entry	Inoculation Treatment						Mean	
	Fungicide Protection		Natural Inoculation		Artificial Inoculation			
	84-85	85-86	84-85	85-86	84-85	85-86	84-85 1/	85-86 2/
1	7289.83	9457.32	6912.31	8918.89	6854.54	8546.86	7018.89A	8974.35
2	6669.57	8863.19	6252.85	7504.38	6952.88	7277.45	6625.10A	7881.67
3	7549.76	10864.25	7438.36	7812.45	7381.98	7339.34	7456.70A	8672.01
4	6773.40	9300.53	6406.19	9116.24	6204.02	7716.86	6461.21A	8711.21
5	7086.97	8090.95	8012.56	7667.35	6194.40	7409.48	7097.97A	7722.59
6	7344.84	8854.25	6391.07	6996.89	6808.47	7079.41	6848.13A	7643.51
7	7639.85	10258.43	7161.93	8020.81	7455.56	7965.11	7419.11A	8748.11
8	8142.52	10779.67	6800.91	8705.02	7066.34	8465.72	7336.59A	9316.80
9	6362.87	8476.03	7275.39	5779.74	6767.90	6765.15	6802.05A	7006.97
10	5779.05	6692.26	6131.82	5481.30	6106.38	4756.51	6005.75A	5643.35
Mean 3/4/	7063.87A	9163.69	6878.34A	7600.31	6779.25A	7332.19		

Std. errors:
(84-85) 1/entry, 447.38; 3/treat., 284.50; entry x treat., 774.88.
(85-86) 2/entry, 167.43; 4/treat., 163.86; entry x treat., 290.00.
Within a year means followed by the same letter are not significantly different at the 0.05 probability level (Fisher's Protected LSD).

interaction between entry and treatment. This information is presented in Table 20. When considering all treatments the highest yielding entry in 1985-86 was the cultivar Hill 81 (entry 8). This cultivar was also one of the highest yielding during 1984-85. Entry 1 was the second highest-yielding line in 1985-86, although this entry yielded close to the average during the 1984-85 cycle. When considering the mean of the three treatments other locally adapted cultivars such as Stephens (entry 7) and Malcolm (entry 3) were for both cycles among the highest yielding entries. Among the lowest yielding entries on both seasons were 9 and 10, two locally developed hard-red selections. Grain yield of entries 1 and 5 was not affected by treatments while entries 3 and 9 suffered large yield reduction from protected to naturally inoculated treatments. Differences between naturally and artificially inoculated treatments were small for most entries with the exception of entries 4 and 10.

Total yield reduction of inoculated compared to protected plots is presented in Table 21. During the 1984-85 growing cycle no reduction was observed for 1000 kernel weight in either of the inoculated treatments. In this cycle the number of seeds per spike was reduced 5% in the artificial inoculated plots. Differences in 1000 kernel weight were found among entries during the 1984-85 cycle. Entries 1, 6, 7, and 8 suffered reductions ranging from 3 to 10% when plots were not protected. Entries 2 and 10 had a reduction in 1000 kernel weight only in artificially inoculated plots. During the 1985-86 cycle 1000 kernel weight was reduced 5 and 6% in naturally and artificially inoculated plots respectively. Number of seeds per spike were also reduced in

Table 21. Mean yield and yield components as a percentage of the control treatment for entries receiving different inoculation treatments in the years 1984-85 and 1985-86.

Entry	Inoculation Treatment											
	Nat.	Art.	Nat.	Art.	Nat.	Art.	Nat.	Art.	Nat.	Art.	Nat.	Art.
	1984-85		1985-86		1984-85		1985-86		1984-85		1985-86	
	Plot grain yield				1000 kernel weight				Seeds per Spike			
1	96	95	94	90	97	97	99	96	98	94	91	93
2	94	104	85	82	103	96	90	95	89	93	94	91
3	98	101	72	68	104	104	86	82	102	89	98	93
4	96	93	99	83	102	101	102	99	94	97	101	96
5	115	88	95	92	103	102	101	99	102	100	93	96
6	88	96	79	80	98	97	94	94	99	89	97	93
7	94	99	78	78	97	92	90	86	108	97	90	92
8	86	90	81	79	93	90	94	90	105	105	98	99
9	124	113	68	80	100	101	98	94	93	95	74	103
10	106	114	82	71	101	97	101	104	100	89	100	96
Mean	97	96	83	80	100	98	95	94	99	95	93	95

these inoculation treatments. Naturally inoculated plots lost 7% of their grains while artificially inoculated plots lost 5%. Plot grain yield was also affected by inoculation treatments in the 1985-86 cycle. Naturally inoculated plots in this season had a yield reduction of 17%. Artificial inoculation increased that yield loss to 20%. Seed yield reduction was also different among entries. All lines, with the exception of 1 and 5, suffered yield reductions that ranged from 32% for entry 3 in artificially inoculated plots to 15% on entry 10 in naturally inoculated plots. Entries 3 and 10 were the most affected by artificial inoculations. Large yield reductions were also observed for naturally inoculated plots of entries 3 and 9. Entries 5 and 1 suffered only slightly yield reductions when they were inoculated. Entry 4 did not suffer a yield reduction when it was naturally inoculated, but a 17% yield loss was observed when it was artificially inoculated.

Correlation coefficients between disease severity either at the flag leaf or at the top four leaves and yield or yield components are presented in Table 22. Higher correlations were generally observed during the 1985-86 than during the 1984-85 growing cycle. This trend was much more consistent in correlations involving disease severity and grain yield. In the 1985-86 season plot grain yield showed a tendency to have higher correlations than either 1000 kernel weight or number of seeds per spike. Entries 1, 4, and 5 had low correlations between yield and disease scored either at the flag or top four leaves. The highest correlation between these variables were found in entries 2, 3, 6, 7, 9, and 10. Entries 3, 6, 7, and 8 had significant correlations

Table 22. Coefficients of correlation between disease severity and yield or yield components for entries grown in the years 1984-85 and 1985-86 (N=9).

Entry	1984-85		1985-86	
	flag leaf	top four	flag leaf	top four
	Seeds per Spike			
1	-0.26	-0.16	-0.66	-0.68*
2	-0.09	-0.26	-0.33	-0.41
3	-0.59	-0.67*	-0.41	-0.45
4	0.32	-0.22	-0.42	-0.24
5	-0.05	-0.07	-0.22	-0.28
6	-0.47	-0.62	-0.55	-0.45
7	-0.43	-0.32	-0.66	-0.65
8	0.35	0.43	-0.11	-0.18
9	-0.04	-0.51	-0.19	-0.34
10	-0.67*	-0.59	-0.23	-0.19
	1000 Kernel Weight			
1	-0.04	-0.05	-0.40	-0.31
2	-0.50	-0.47	-0.68*	-0.64
3	0.18	0.46	-0.90**	-0.88**
4	-0.43	0.03	-0.39	-0.09
5	0.04	0.06	-0.11	-0.07
6	-0.32	-0.78*	-0.79**	-0.83*
7	-0.43	-0.54	-0.89**	-0.88**
8	-0.50	-0.71*	-0.95**	-0.91**
9	-0.18	0.01	-0.50	-0.42
10	-0.68*	-0.51	0.50	0.45
	Grain Yield			
1	-0.20	-0.27	-0.69*	-0.69*
2	0.40	0.25	-0.87**	-0.88**
3	-0.19	-0.06	-0.95**	-0.95**
4	-0.42	-0.50	-0.76*	-0.58
5	-0.28	-0.12	-0.80**	-0.77*
6	-0.31	-0.35	-0.91**	-0.94**
7	0.10	0.01	-0.89**	-0.88**
8	-0.16	-0.26	-0.83**	-0.90**
9	0.06	0.10	-0.65	-0.78*
10	0.18	0.14	-0.94**	-0.93**

Coefficients followed by ** and * are significantly different from "0" at the 0.01 and 0.05 probability levels respectively.

between disease severity and 1000 kernel weight. Only entry 1 had significant correlation between disease severity and seeds per spike.

Grain hardness and grain protein percent were not affected by septoria tritici blotch in either year. During the 1984-85 growing cycle entries showed a tendency to have higher grain hardness as well as higher grain protein percent than in 1985-86. A summary of the data obtained for grain hardness and protein percent is presented in Table 23.

On the 1985-86 growing cycle test weight was also included in the analysis. Protected plots had higher test weight than inoculated plots. Entry differences were also found for this variable. The highest test weight was found for entry 5 followed by entry 4. Entries 3 and 6 had the lowest test weight. Results found for the variable test weight are presented in Table 24.

Blocking seemed to have been successful in removing variation in at least two occasions. During the 1984-85 growing cycle grain hardness in replication 1 was higher than in the other replications. On the 1985-86 cycle the number of seeds per spike in replication 1 was larger than in the other two replications.

Study 3

Effect of Planting Date and Inoculation Procedures on Field Grown Wheat

Weather conditions prevailing during the 1984-85 and 1985-86 growing cycles in which this experiment was performed were the same as those described for Study 2. In this study all variables produced

Table 23. Mean grain hardness and protein percent for entries grown in the years 1984-85 and 1985-86.

Entry	Hardness		Protein (%)	
	1984-84	1985-86	1984-85	1985-86
1	107.4	96.2	10.6	9.5
2	62.2	63.4	11.0	9.5
3	57.6	44.7	9.7	8.8
4	125.3	117.4	11.6	9.5
5	112.9	104.5	11.1	10.4
6	137.9	122.5	10.7	9.6
7	50.2	43.6	9.9	8.7
8	56.7	47.4	9.6	9.0
9	137.9	116.9	10.8	10.6
10	101.4	106.4	13.7	13.1
Mean1/ 2/	95.0	86.3	10.9	9.9

Standard errors:
(1984-85) 1/hardness, 3.52; protein, 0.32.
(1985-86) 2/hardness, 2.97; protein, 0.23.

Table 24. Mean seed test weight (kg/hl) for entries receiving different inoculation treatments in the year 1985-86.

Entry	Inoculation Treatment			Mean
	Fungicide Protection	Natural Inoculation	Artificial Inoculation	
1	80.2	79.6	79.5	79.8 c
2	80.4	80.6	79.1	79.9 c
3	79.8	76.9	76.6	77.8 d
4	82.5	81.5	81.2	81.7 b
5	83.1	83.1	82.8	83.0 a
6	79.3	77.8	76.6	77.9 d
7	80.9	79.5	79.8	80.0 c
8	80.4	79.6	79.6	79.9 c
9	81.0	78.7	79.6	79.7 c
10	80.6	79.7	79.5	80.0 c
Mean	80.8 a	79.6 b	79.4 b	

Means followed by the same letter are not significantly different at the 0.01 probability level (Fisher's Protected LSD).

homogeneous error variances between years as measured by the F test. Consequently, a combined analysis of years was performed for each variable measured.

Treatments will be cited during this discussion by their number designation. Treatment 1 refers to late sown plots (Jan. 20) which were covered with a plastic film after artificial inoculations. Treatment 2 was sown late (Jan. 20) and was artificially inoculated, while treatment 3 was also sown late (Jan. 20) but it was naturally inoculated. Treatment 4 was sown early (Sept. 25) and artificially inoculated. Treatment 5 was sown at the recommended or normal planting date for the region (Oct. 25) and was also artificially inoculated.

Differences were detected among entries, treatments, and years, for number of seeds per spike. However, because of the high interaction between these three factors, results are presented for each year separately. Table 25 shows the results found for the number of seeds per spike.

During the 1984-85 cycle plots in treatment 5 had a higher number of seeds per spike than plots in the other treatments. Due to the high interaction between entry and treatment, entries had to be studied individually for each treatment. The number of seeds per spike increased for all entries when treatment 4 is compared to treatment 5. An increase in the number of seeds per spike was observed for entries 1, 2, and 5, in treatment 1 compared to treatment 3 while other entries did not show an increase for the same comparison. Entries 2, 6, and the cultivar Stephens (entry 7) had a large increase in the number of seeds per spike for treatment 1 compared to treatment 5, while entries

Table 25. Mean number of seeds per spike in entries sown at different dates and receiving various *Septoria tritici* inoculation treatments in 1984-85 and 1985-86.

Treat	Year	Entry 1	2	3	4	5	6	7	8	9	10	Mean 2/4/
1	84-85	60.69	69.13	65.83	63.37	59.00	69.60	62.70	73.33	60.63	55.77	64.01
	85-86	68.70	69.53	65.67	76.13	71.57	85.23	66.60	79.57	63.70	65.90	71.26
2	84-85	61.93	66.27	68.10	67.53	61.30	73.07	64.33	70.60	65.87	55.13	65.41
	85-86	67.93	70.70	71.03	73.53	69.80	81.23	63.30	77.77	62.60	66.67	70.46
3	84-85	64.00	70.23	64.53	65.27	63.80	69.83	62.40	71.73	63.13	55.93	65.09
	85-86	69.17	71.53	67.93	73.50	72.33	75.60	63.30	72.43	63.00	65.80	69.46
4	84-85	68.47	62.30	60.70	70.73	64.00	71.80	54.63	76.33	62.30	57.33	64.86
	85-86	73.57	76.27	79.10	89.30	74.77	92.83	64.00	87.40	60.93	60.67	75.88
5	84-85	75.40	81.13	71.10	79.00	79.53	90.27	70.20	82.17	73.93	66.70	76.94
	85-86	69.57	71.93	75.43	78.40	67.47	81.37	73.93	94.90	64.10	60.43	73.75
Mean 1/ 3/	84-85	61.93	69.81	66.05	69.18	65.53	74.91	62.85	74.83	65.17	58.17	
	85-86	69.79	71.99	71.83	78.17	71.19	83.25	66.23	82.41	62.87	63.89	

Std. errors: (84-85) 1/entry, 1.04; 2/treat., 1.15; entry x treat., 2.34.
(85-86) 3/entry, 1.37; 4/treat., 1.02; entry x treat., 3.06.
Treatments: 1=late sown, plastic cover, 2=late sown, artificial inoculation, 3=late sown, natural inoculation, 4=early sown, artificial inoculation 5=recommended sowing date, artificial inoculation.

1, 4, 10, and the cultivar Hill 81 (entry 8) showed a smaller increase.

In the 1985-86 growing season treatment 4 had the highest number of seeds per spike followed by treatment 5. All treatments with the exception of treatment 5 had more seeds per spike during 1985-86 than in the 1984-85 cycle. Differences were also noted among entries and for the interaction between treatment and entry. A decrease in the number of seeds per spike was noted for entries 9 and 10 when treatment 3 is compared to treatment 4. With the exception of entry 9 all other entries had more seeds per spike during the 1985-86 than 1984-85 cycle. The grand mean for the 1984-85 cycle was 67.26 against 72.16 grains per spike during 1985-86.

Differences were found in the weight of 1000 kernels among years, entries, treatments, and among all interactions. Information on 1000 kernel weight is presented in Table 26. During 1984-85 the heaviest seeds were found in treatments 3, 4, and 5. The lightest seeds were produced in treatment 1. Some entries, such as 1, 4 and the cultivar Hill 81 (entry 8) showed small differences between treatments 1 and 3. The largest difference between these two treatments was found for the cultivar Malcolm (entry 3).

In the 1985-86 season, smaller differences were found among treatments. The heaviest seeds were produced in treatments 4 and 5 and the lightest seeds were produced in treatment 3. Interaction between treatment and entry was mainly the effect of differences in seed weight increase among entries when treatments 1, 2, or 3 are compared to treatments 4 or 5. Entries 3, 4, and 8 had small changes in kernel weight from treatment to treatment, while entries 1 and 5 had larger

Table 26. Mean 1000 kernel weight (g) of entries sown at different dates and receiving various *Septoria tritici* inoculation treatments in 1984-85 and 1985-86.

Treat	Year	Entry 1	2	3	4	5	6	7	8	9	10	Mean 2/ 4/
1	84-85	40.72	40.77	45.77	36.56	42.41	42.11	48.19	37.47	42.24	46.38	42.26
	85-86	42.43	40.58	44.90	38.72	44.24	38.43	45.68	35.21	39.71	44.84	41.47
2	84-85	41.43	43.72	49.32	38.20	43.88	45.37	53.14	38.93	44.35	49.14	44.75
	85-86	41.58	40.21	44.76	38.69	42.97	37.39	45.24	35.60	42.24	44.95	41.36
3	84-85	41.92	45.78	53.25	38.07	46.36	46.17	52.89	40.22	47.41	50.14	46.22
	85-86	40.05	37.84	43.72	37.91	42.42	35.96	44.77	34.54	37.25	45.40	39.97
4	84-85	46.12	42.40	49.74	40.49	47.03	45.05	55.75	45.17	44.94	49.53	46.62
	85-86	45.93	38.89	43.37	37.82	50.58	41.84	53.00	39.13	43.33	45.00	43.89
5	84-85	43.63	47.13	55.43	39.23	45.98	47.72	51.75	40.13	46.29	51.33	46.86
	85-86	46.71	39.65	44.57	38.19	49.26	37.60	51.09	37.58	38.35	47.77	43.08
Mean 1/ 3/	84-85	42.76	43.96	50.70	38.51	45.13	45.28	52.34	40.38	45.05	49.30	
	85-86	43.34	39.44	44.26	38.26	45.89	38.24	47.96	36.41	40.18	45.59	

Std. errors: (84-85) 1/entry, 0.45; 2/treat., 0.75; entry x treat., 1.01.
(85-86) 3/entry, 0.60; 4/treat., 0.67; entry x treat., 1.35.
Treatments: 1=late sown, plastic cover, 2=late sown, artificial inoculation, 3=late sown, natural inoculation, 4=early sown, artificial inoculation 5=recommended sowing date, artificial inoculation.

changes in kernel weight between treatments. The overall experiment mean for 1984-85 was 45.34 g and for 1985-86 it was 41.96 g. As the number of seeds per spike increased from 1984-85 to 1985-86, kernel weight decreased in the same time frame.

Variability was found for grain hardness among entries, however, no effect of years nor treatments were noted. Because of the significance of the higher order interaction, results are presented separately in Table 27 for each growing cycle. Grain hardness for 1984-85 was 84.41 against 86.11 during 1985-86. The largest increase between cycles was noted in treatments 3 and 5. Entry by year interaction was mainly the effect of entries 1, 9, 10, and 4. Of these, the first three entries had a reduction in grain hardness from 1984-85 to 1985-86. Entry 4 showed an increase of 12 hardness units from 1984-85 to 1985-86.

Grain protein percentage was modified by years and entries, however it was not affected by treatments. The entry by year and entry by treatment interactions were also significant. Table 28 presents information on grain protein percentage for entries in the 1984-85 and 1985-86 growing cycles. During 1984-85 there were small differences between hard- (entries 1, 2, 4, 5, 6, 9, and 10) and soft-type (entries 3, 7, and 8) entries, however, these differences were more apparent during 1985-86. During the second growing season, grain protein percent was reduced by 1.19% compared with the previous cycle.

Disease severity levels recorded in the top four leaves and flag leaves during the last sampling date in the 1984-85 and 1985-86 cycles are presented in Tables 29 and 30. Septoria severity measured at this

Table 27. Mean grain hardness in entries sown at different dates and receiving various *Septoria tritici* inoculation treatments in 1984-85 and 1985-86.

Entry	Treatment 1	2	3	4	5	Mean 1/3/
			1984-85			
1	95.80	106.07	97.53	107.90	96.07	100.67
2	50.43	46.50	48.77	53.70	48.03	49.49
3	42.37	34.90	36.07	56.40	38.63	41.67
4	104.07	109.00	96.83	114.03	103.97	105.58
5	94.37	105.37	96.70	95.17	92.77	96.87
6	140.70	117.77	115.87	132.87	133.43	128.13
7	41.33	33.73	35.13	51.47	45.47	41.43
8	50.40	39.67	39.07	44.87	43.60	43.52
9	139.53	132.30	142.90	139.03	136.87	138.13
10	98.33	102.13	95.23	99.80	97.63	98.63
Mean2/	85.73	82.74	80.41	89.52	83.65	
			1985-86			
1	86.10	86.10	78.87	94.53	108.43	90.81
2	51.07	51.07	50.93	58.10	58.93	54.02
3	54.60	44.93	45.93	38.90	50.33	46.94
4	109.07	119.90	126.33	109.57	123.93	117.76
5	86.80	112.33	84.40	102.27	100.83	97.33
6	128.13	144.47	122.03	130.57	145.63	134.17
7	35.63	39.93	44.60	34.17	50.80	41.03
8	50.13	45.63	49.30	52.67	43.30	48.21
9	129.70	134.43	116.80	127.27	118.93	125.43
10	101.53	103.73	101.27	109.63	110.90	105.41
Mean4/	83.28	88.25	82.05	85.77	91.20	

Std. errors: (84-85) 1/entry, 2.37; 2/treat., 2.86;
entry x treat., 5.31.
(85-86) 3/entry, 2.69; 4/treat., 3.81;
entry x treat., 6.02.

Treatments: 1=late sown, plastic cover, 2=late sown, artificial inoculation, 3=late sown, natural inoculation, 4=early sown, artificial inoculation, 5=recommended sowing date, artificial inoculation.

Table 28. Mean grain protein percent in entries sown at different dates and receiving various *Septoria tritici* inoculation treatments in 1984-85 and 1985-86.

Entry	Treatment 1	2	3	4	5	Mean 1/3/
			1984-85			
1	11.40	12.07	11.80	11.17	11.80	11.65
2	11.23	10.87	11.17	10.57	11.37	11.04
3	10.57	10.50	10.40	9.33	10.63	10.29
4	11.93	12.27	11.97	11.87	10.77	11.76
5	10.40	10.57	10.53	12.13	11.77	11.08
6	12.23	11.33	11.77	11.83	12.27	11.89
7	10.73	10.63	10.90	9.57	9.87	10.34
8	9.93	10.67	10.60	10.13	10.70	10.41
9	11.07	10.93	11.33	11.17	12.20	11.34
10	13.40	13.43	13.47	13.13	13.67	13.42
Mean2/	11.29	11.33	11.39	11.09	11.50	
			1985-86			
1	9.73	9.47	9.57	10.37	10.13	9.85
2	9.97	10.53	10.13	10.53	9.93	10.22
3	8.83	9.33	9.13	9.43	9.13	9.17
4	11.97	11.37	11.60	10.43	10.30	11.13
5	9.93	9.93	9.70	10.60	10.57	10.15
6	10.00	10.00	9.80	10.03	9.97	9.96
7	9.50	8.87	9.00	9.13	9.13	9.13
8	9.57	9.20	9.10	8.90	9.20	9.19
9	9.83	9.77	9.73	11.10	10.10	10.11
10	11.87	12.37	12.40	12.67	12.63	12.39
Mean4/	10.12	10.08	10.02	10.32	10.11	

Std. errors: (84-85) 1/entry, 0.17; 2/treat., 0.23;
entry x treat., 0.38.
(85-86) 3/entry, 0.15; 4/treat., 0.15;
entry x treat., 0.33.

Treatments: 1=late sown, plastic cover, 2=late sown, artificial inoculation, 3=late sown, natural inoculation, 4=early sown, artificial inoculation, 5=recommended sowing date, artificial inoculation.

Table 29. Percentage of top four leaves area destroyed by *Septoria tritici* in entries sown at different dates and receiving various *Septoria tritici* inoculation treatments in 1984-85 and 1985-86.

Treat	Year	Entry 1	2	3	4	5	6	7	8	9	10	Mean 2/ 4/
1	84-85	60.00	86.67	81.67	68.33	83.33	75.00	91.67	66.67	73.33	85.00	77.17
	85-86	53.33	88.33	83.33	66.67	80.00	73.33	93.33	70.00	83.33	88.33	78.00
2	84-85	36.67	78.33	63.33	45.00	70.00	46.67	70.00	55.00	60.00	70.00	59.50
	85-86	48.33	86.67	81.67	56.67	73.33	66.67	85.00	70.00	78.33	76.67	72.33
3	84-85	10.00	36.67	16.67	8.33	18.33	16.67	30.00	26.67	20.00	30.00	21.33
	85-86	45.00	80.00	80.00	46.67	70.00	56.67	83.33	68.33	73.33	76.67	68.00
4	84-85	55.00	76.67	80.00	58.33	73.33	51.67	95.00	68.33	61.67	73.33	69.33
	85-86	88.33	91.67	96.67	68.33	83.33	73.33	98.33	83.33	85.00	76.67	84.50
5	84-85	50.00	70.00	66.67	46.67	60.00	58.33	85.00	58.33	65.00	73.33	63.33
	85-86	81.67	83.33	86.67	68.33	80.00	66.67	96.67	76.67	86.67	76.67	80.33
Mean 1/ 3/	84-85	42.33	69.67	61.67	45.33	61.00	49.67	74.33	55.00	56.00	66.33	
	85-86	63.33	86.00	85.67	61.33	77.33	67.33	91.33	73.67	81.33	79.00	

Std. errors: (84-85) 1/entry, 2.32; 2/treat., 2.45; entry x treat., 5.19.
(85-86) 3/entry, 1.50; 4/treat., 1.46; entry x treat., 3.35.
Treatments: 1=late sown, plastic cover, 2=late sown, artificial inoculation, 3=late sown, natural inoculation, 4=early sown, artificial inoculation, 5=recommended sowing date, artificial inoculation.

Table 30. Percentage of flag leaf area destroyed by *Septoria tritici* in entries sown at different dates and receiving various *Septoria tritici* inoculation treatments in 1984-85 and 1985-86.

Treat	Year	Entry 1	2	3	4	5	6	7	8	9	10	Mean 2/ 4/
1	84-85	35.00	65.00	50.00	25.00	80.00	31.67	68.33	21.67	33.33	53.33	46.33
	85-86	43.33	70.00	70.00	26.67	66.67	36.67	73.33	23.33	43.33	53.33	50.67
2	84-85	6.67	46.67	26.67	11.67	43.33	15.00	35.00	15.00	13.33	31.67	24.50
	85-86	33.33	56.67	63.33	16.67	56.67	20.00	66.67	26.67	40.00	36.67	41.67
3	84-85	0.67	5.33	3.67	1.00	3.67	3.67	5.33	1.00	2.33	6.67	3.33
	85-86	33.33	53.33	56.67	13.33	43.33	16.67	63.33	25.00	36.67	33.33	37.50
4	84-85	13.33	61.67	73.33	18.33	46.67	10.00	93.33	15.00	53.33	50.00	43.50
	85-86	53.33	76.67	86.67	33.33	66.67	33.33	86.67	56.67	63.33	43.33	60.00
5	84-85	11.67	33.33	38.33	11.67	25.00	13.33	53.33	13.33	20.00	30.00	25.00
	85-86	26.67	53.33	73.33	18.33	53.33	26.67	83.33	53.33	56.67	40.00	48.50
Mean 1/ 3/	84-85	13.47	42.40	38.40	13.53	39.73	14.73	51.07	13.20	24.47	34.33	
	85-86	38.00	62.00	70.00	21.67	57.33	26.67	74.67	37.00	48.00	41.33	

Std. errors: (84-85) 1/entry, 2.26; 2/treat., 1.83; entry x treat., 5.04.
(85-86) 3/entry, 1.95; 4/treat., 1.68; entry x treat., 4.36.
Treatments: 1=late sown, plastic cover, 2=late sown, artificial inoculation, 3=late sown, natural inoculation, 4=early sown, artificial inoculation, 5=recommended sowing date, artificial inoculation.

last sampling date at the top four leaves was different among treatments and entries. Differences were also noted for the entry by treatment interaction in the 1985-86 season. Disease severity measured at the flag leaf was different for both growing seasons among treatments, entries, and for the entry by treatment interaction. Disease severity was constantly higher during 1985-86 compared to 1984-85 regardless of the leaf level measured. The largest difference between cycles was recorded for disease severity in the flag leaves. The lowest difference between cycles was noted in treatment 1 and the largest differences observed in treatment 3. For both seasons, entries 1, 4, and 6 had the lowest disease severity at either leaf level. Entries 2 and 7 had the highest levels of disease in either cycle. Line 3 had the highest disease severity during 1985-86 but it was near the mean of the entries during 1984-85. As was indicated by the significance of the entry by treatment interaction, not all entries increased or reduced in disease severity for each treatment in a similar way.

Data recorded for each plot for the variables top four and flag leaves disease severity, and disease progress index were regressed against sampling dates using the simple linear regression model. The regression coefficients obtained for each variable were then used as observations in analysis of variances.

Significant differences were found for the regression coefficients of disease severity in the top four leaves versus time among years, treatments, and entries. Also significant interactions of treatment by year and entry by treatment were noted. Information on the interaction

between treatment and entry is presented in Table 31. Table 32 includes the interaction between year and treatment for the regression coefficient of disease severity in the top four leaves versus time. Large values for the regression coefficients describes a faster rate of disease increase through time. Entries 2 and 7 followed by 10 and 3 had higher rates of disease increase than those observed for the other entries. Entries 1, 4, and 6 had the lowest rate of septoria tritici blotch progress. The rate of disease severity change between treatments was not the same for all entries. Entries had the highest rate of disease progress in treatment 1 and the lowest in treatment 3. Most entries had in treatment 2 values similar to those of treatment 5. Entry 1 had a lower coefficient in treatment 2 than in treatment 5. Conversely, entry 2 had a higher rate in treatment 2 than in treatment 5.

During 1985-86 the rate of disease progress was higher than during 1984-85, although, the increase in rate from one cycle to another was different for each treatment. The largest increase in disease progress rate between growing cycles was observed for treatment 3. Treatments 2, 4, and 5 showed a moderate rate of increase from one cycle to another. While treatment 1 had the same disease progress rate in both growing seasons.

Disease progress in the flag leaf was also regressed versus time and the regression coefficients used as observations in the analysis of variance. The analysis of these coefficients indicated a significant difference among treatments, entries, years, and for the interactions among these factors. Table 33 shows the results found for the

Table 31. Regression coefficient of disease severity at the top four leaves vs. time for the combined analysis of years in entries sown at different dates and receiving various *Septoria tritici* inoculation treatments in 1984-85 and 1985-86 (N=6).

Entry	Treatment					Mean 1/
	1	2	3	4	5	
1	0.828	0.563	0.344	0.941	0.802	0.695
2	1.418	1.279	0.861	1.053	1.046	1.131
3	1.239	0.952	0.615	1.180	1.048	1.007
4	1.033	0.717	0.338	0.839	0.824	0.750
5	1.226	1.023	0.600	0.978	0.947	0.955
6	1.142	0.854	0.505	0.998	0.989	0.897
7	1.337	1.090	0.777	1.251	1.210	1.133
8	1.023	0.904	0.665	1.030	0.926	0.909
9	1.155	0.961	0.607	0.942	1.021	0.936
10	1.374	1.126	0.809	1.033	1.066	1.081
Mean 2/	1.177	0.947	0.612	1.024	0.988	

Std. errors: 1/entry, 0.0237; 2/treat., 0.0291;
entry x treat., 0.0529.
Treatments: T1=late sown, plastic cover, T2=late sown, artificial inoculation, T3=late sown, natural inoculation, T4=early sown, artificial inoculation, T5=recommended sowing date, artificial inoculation.

Table 32. Coefficients of regression between disease severity at the top four leaves vs. time for the different dates and *Septoria tritici* inoculation treatments in the years 1984-85 and 1985-86 (N=6).

Treatment	Year	
	1984-85	1985-86
1	1.188	1.167
2	0.882	1.011
3	0.280	0.945
4	0.978	1.070
5	0.940	1.035
Mean 1/	0.854	1.046

Std. errors: 1/year, 0.0142; year x treat., 0.0412.
Treatments: T1=late sown, plastic cover, T2=late sown, artificial inoculation, T3=late sown, natural inoculation, T4=early sown, artificial inoculation, T5=recommended sowing date, artificial inoculation.

regression coefficients of flag leaf disease progress versus time. As with the disease progress measured in the top four leaves, flag leaves disease progress was greater in the 1985-86 growing cycle. The largest increase was observed in treatment 3 and the lowest in treatment 1. A relatively large disease progress rate increase was observed for treatment 5 from 1984-85 to 1985-86 compared with the rate of increase in the top four leaves. With the exception of entry 10 for other entries there was an increase in flag leaf disease progress rate from 1984-85 to 1985-86. Entry 3 had the largest increase between cycle while entries 4, 6, and 10 had the lowest.

The variable disease progress index was computed by dividing the height at which septoria tritici blotch was observed in the plant by plant height with the subsequent value being regressed against time. Results obtained for the analysis of this coefficient for the combined analysis of years are found in Table 34. Significant variation was found for disease progress index among treatments, entries, treatment by entry, and treatment by year interactions. Treatment 1 had the highest rate of disease progress index while treatments 3, 4, and 5 had the lowest rate of disease progress index. The treatment by entry interaction was mainly the effect of entries, such as 4 and 6, which maintained relative stable coefficients between treatments 1 and 2. Changes in the coefficient were noted between these two treatments for other entries. Entries 2, 3, 6, and 8 had the highest regression coefficient for this variable and entries 4, 5, 9, and 10 the lowest. The largest decrease between cycles were observed for entry 4. The overall experiment means between growing cycles were not different.

Table 33. Coefficients of the regression between disease severity at the flag leaf vs. time in entries sown at different dates and receiving various *Septoria tritici* inoculation treatments in 1984-85 and 1985-86 (N=6).

Entry	Treatment 1	2	3	4	5	Mean 1/ 3/
			1984-85			
1	0.361	0.067	0.006	0.217	0.126	0.155
2	0.771	0.507	0.056	1.014	0.400	0.550
3	0.658	0.291	0.036	1.191	0.404	0.516
4	0.257	0.115	0.010	0.298	0.117	0.159
5	0.905	0.436	0.036	0.760	0.269	0.481
6	0.339	0.158	0.036	0.163	0.175	0.174
7	0.770	0.374	0.052	1.535	0.606	0.667
8	0.214	0.152	0.010	0.244	0.184	0.161
9	0.338	0.134	0.023	0.861	0.237	0.318
10	0.745	0.362	0.065	0.822	0.480	0.495
Mean 2/	0.536	0.260	0.033	0.710	0.300	0.368
			1985-86			
1	0.478	0.314	0.312	0.672	0.326	0.421
2	0.813	0.649	0.622	1.130	0.764	0.796
3	0.824	0.667	0.643	1.312	0.943	0.878
4	0.277	0.159	0.126	0.445	0.192	0.240
5	0.846	0.644	0.470	0.911	0.712	0.717
6	0.487	0.237	0.176	0.392	0.269	0.312
7	0.839	0.731	0.700	1.348	1.039	0.931
8	0.291	0.300	0.286	0.606	0.551	0.407
9	0.527	0.455	0.391	0.821	0.658	0.570
10	0.640	0.445	0.350	0.489	0.416	0.468
Mean 4/	0.602	0.460	0.408	0.813	0.587	0.574

Std. errors: (84-85) 1/entry, 0.0301; 2/treat., 0.0222; entry x treat., 0.0672.
(85-86) 3/entry, 0.0258; 4/treat., 0.0273; entry x treat., 0.0578.

Treatments: T1=late sown, plastic cover, T2=late sown, artificial inoculation, T3=late sown, natural inoculation, T4=early sown, artificial inoculation, T5=recommended sowing date, artificial inoculation.

Table 34. Coefficients of the regression between disease progress index vs. time in entries sown at different dates and receiving various *Septoria tritici* inoculation treatments in 1984-85 and 1985-86 (N=6).

Entry	Treatment 1	2	3	4	5	Mean 1/ 3/
			1984-85			
1	0.833	0.644	0.248	0.504	0.516	0.549
2	1.072	0.920	0.445	0.427	0.725	0.718
3	1.147	0.889	0.473	0.526	0.523	0.712
4	0.963	0.775	0.333	0.473	0.611	0.631
5	0.884	0.639	0.285	0.498	0.491	0.560
6	0.724	0.567	0.320	0.563	0.699	0.575
7	0.917	0.592	0.281	0.502	0.468	0.552
8	0.965	0.790	0.553	0.300	0.663	0.654
9	0.963	0.822	0.345	0.502	0.383	0.603
10	0.894	0.712	0.524	0.375	0.547	0.610
Mean 2/	0.936	0.735	0.381	0.467	0.563	0.616
			1985-86			
1	0.867	0.754	0.545	0.655	0.483	0.661
2	0.982	0.823	0.838	0.479	0.393	0.703
3	0.882	0.788	0.579	0.591	0.514	0.671
4	0.749	0.662	0.478	0.356	0.151	0.479
5	0.670	0.728	0.521	0.415	0.359	0.539
6	0.943	1.056	0.929	0.716	0.504	0.829
7	0.729	0.770	0.637	0.540	0.455	0.626
8	0.898	0.665	0.735	0.337	0.337	0.595
9	0.700	0.462	0.530	0.626	0.356	0.535
10	0.875	0.659	0.681	0.415	0.255	0.577
Mean 4/	0.829	0.737	0.647	0.513	0.381	0.621

Std. errors: (84-85) 1/entry, 0.035; 2/treat., 0.044; entry x treat., 0.078.
(85-86) 3/entry, 0.036; 4/treat., 0.034; entry x treat., 0.080.

Treatments: T1=late sown, plastic cover, T2=late sown, artificial inoculation, T3=late sown, natural inoculation, T4=early sown, artificial inoculation, T5=recommended sowing date, artificial inoculation.

From 1984-85 to 1985-86, treatment 3 had the largest increase in disease progress index rate . During the same period, treatment 5 showed a decrease. Treatments 1 and 4 maintained a more or less constant disease progress index rate for both growing cycles.

Another way of studying the relationship between plant height and the height of the disease was to regress these two variables using plant height as the independent variable. Table 35 shows the regression coefficients obtained for this relationship. The analysis of this variable indicated significant differences among years, treatments, entries, and among all interactions. Treatment 4 had for the 1984-85 as well as for the 1985-86 cycle the most rapid vertical development of the disease and treatment 3 the slowest. Differences were not found during any growing cycle among treatments 1, 2, and 5. During the 1984-85 cycle treatments 1 and 2 were different from treatment 3. For both growing seasons the most rapid movement of the disease up the plant was found for entries 2, 3, and 7 while entries 1 and 8 had the slowest. The decrease in disease progress index rate observed from treatment 1 to treatment 3 was not uniform for all entries. Also the increase in disease progress index rate observed between treatments 3 and 4 or 5 was not uniform. These differences contributed to the significance of the entry by treatment interaction.

Study 4

Effect of *Septoria tritici* on Selected Morphologic and Physiologic Characters of Wheat During the 1985-1986 Crop Season

Each entry was sampled seven times during the 1985-86 growing

Table 35. Coefficient of the regression between plant height vs. disease height in entries sown at different dates and receiving various *Septoria tritici* inoculation treatments in 1984-85 and 1985-86 (N=6).

Entry	Treatment 1	2	3	4	5	Mean 1/ 3/
			1984-85			
1	0.677	0.500	0.249	0.986	0.805	0.643
2	0.916	0.813	0.441	1.147	0.934	0.850
3	0.964	0.754	0.387	1.397	0.758	0.852
4	0.779	0.626	0.270	0.953	0.626	0.651
5	0.845	0.611	0.305	1.094	0.721	0.715
6	0.739	0.649	0.312	1.133	0.861	0.739
7	0.880	0.692	0.461	1.448	1.006	0.897
8	0.710	0.598	0.394	0.864	0.856	0.684
9	0.876	0.704	0.380	1.298	0.664	0.785
10	0.838	0.687	0.423	1.128	0.916	0.798
Mean 2/	0.822	0.663	0.362	1.145	0.815	0.761
			1985-86			
1	0.875	0.778	0.579	1.413	0.936	0.916
2	0.999	0.950	0.955	1.250	1.125	1.056
3	0.984	0.926	0.819	1.571	1.226	1.105
4	0.729	0.682	0.542	0.871	0.650	0.695
5	0.815	0.836	0.682	1.084	0.955	0.874
6	0.990	1.079	1.009	1.525	1.006	1.122
7	1.002	1.013	0.916	1.497	1.250	1.136
8	0.807	0.731	0.685	0.990	0.910	0.825
9	0.839	0.703	0.665	1.584	1.047	0.968
10	1 039	0.886	0.857	1.183	0.856	0.964
Mean 4/	0.908	0.859	0.771	1.297	0.996	0.966

Std. errors: (84-85) 1/entry, 0.025; 2/treat., 0.040; entry x treat., 0.057.
(85-86) 3/entry, 0.029; 4/treat., 0.035; entry x treat., 0.066.

Treatments: T1=late sown, plastic cover, T2=late sown, artificial inoculation, T3=late sown, natural inoculation, T4=early sown, artificial inoculation, T5=recommended sowing date, artificial inoculation.

cycle. Analysis of variances carried out for each of the sampling dates yielded information on the magnitude of the different experimental error variances. Tests for variance homogeneity across sampling dates were carried for stem length, stem dry weight, stem dry weight by unit of length, spike dry weight, top four leaves dry weight, ratio between flag leaf diseased area and flag leaf total area, dry stems monosaccharide and disaccharide content, stem phloem exudate monosaccharide and disaccharide content, and flag leaf phloem exudate monosaccharide and disaccharide content. Variables which had homogeneous variances among sampling dates were analyzed including time of observation as a factor in the experiment. Variables which had heterogeneous variance among sampling date were investigated for the presence of any functional relationship between the variance and the mean of each sampling date. Proper conversion methods were used when the relationship between the mean and the variance was established. Variables in which a functional relationship could not be established were analyzed independently for each sampling date.

Error mean squares for stem length were homogeneous among sampling dates. Significant differences were found for this variable among treatments, entries, time of observation, and for the entry x time of observation interaction. Information on stem length recorded at each sampling date can be found in Table 36. Plots in the fungicide-protected treatment had an overall stem length mean of 93.9 cm. These stems were significantly shorter than those of plots either naturally or artificially inoculated were a mean value of 97.5 and 98.3 cm were obtained respectively. Interaction between entry and time of

Table 36. Mean stem length (cm) at different sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated and grown in 1985-86.

Sampling Treat. Date	Entry 1	3	4	5	7	10	Mean1/
Protec. 1	77.29	72.92	64.07	83.97	76.17	91.78	77.70
Nat. Inoc.	76.65	75.85	68.43	89.96	78.45	92.99	80.39
Artif.Inoc.	80.43	81.50	68.89	90.71	81.75	91.83	82.52
Mean 2/	78.13	76.76	67.13	88.21	78.79	92.20	
Protec. 2	79.34	93.32	85.83	96.63	92.53	106.28	92.32
Nat. Inoc.	85.19	94.11	93.98	99.87	95.59	108.79	96.26
Artif.Inoc.	85.25	96.10	92.89	99.25	99.01	109.81	97.05
Mean	83.26	94.51	90.90	98.58	95.71	108.29	
Protec. 3	79.90	95.00	90.75	102.27	96.75	111.07	95.96
Nat. Inoc.	84.95	95.97	99.39	104.55	99.78	113.05	99.62
Artif.Inoc.	85.76	95.05	98.49	107.01	99.48	113.62	99.90
Mean	83.54	95.34	96.21	104.61	98.67	112.58	
Protec. 4	82.21	95.31	94.91	101.25	97.77	109.77	96.87
Nat. Inoc.	84.56	97.71	98.99	107.84	108.01	111.15	101.37
Artif.Inoc.	84.70	98.92	97.17	107.39	106.91	113.88	101.50
Mean	83.82	97.31	97.02	105.49	104.23	111.60	
Protec. 5	81.19	95.80	91.87	106.73	97.90	111.38	97.48
Nat. Inoc.	85.31	100.79	96.53	105.58	103.16	115.91	101.21
Artif.Inoc.	85.72	98.64	99.45	105.11	105.83	112.34	101.18
Mean	84.08	98.41	95.95	105.81	102.30	113.21	
Protec. 6	82.38	96.71	96.15	106.98	104.25	110.24	99.45
Nat. Inoc.	84.02	99.50	100.03	105.67	105.38	112.50	101.18
Artif.Inoc.	86.09	99.41	100.19	106.01	107.24	115.41	102.39
Mean	84.16	98.54	98.79	106.22	105.62	112.72	
Protec. 7	82.04	100.76	94.67	102.99	97.05	109.07	97.76
Nat. Inoc.	87.84	98.38	103.66	108.87	103.89	115.63	103.04
Artif.Inoc.	87.60	100.83	103.45	108.27	103.73	118.13	103.67
Mean	85.83	99.99	100.59	106.71	101.56	114.28	

Std. errors: 1/sampling date x treat.,0.69; 2/sampling date x entry, 0.97; sampling date x entry x treat., 1.69.

observation was mainly due to entry 1 which had nearly reached its full height at the time of the first sampling date. Stem length recorded during the last sampling date could be considered as the final height reached by each entry during the growing season. Entry 10 was the tallest at 114 cm, followed by entry 5 at 107 cm. Entries 3, 4, and 7 were approximately 100 cm tall and entry 1 was the shortest at 86 cm.

Error variances for the variable stem dry weight were homogeneous among sampling dates. The analysis of this variable revealed differences among entries, time of observation, entry by treatment, and entry by time of observation interactions. The results found for stem dry weight are presented in Table 37. Entries varied in the way stem dry weight was modified as a result of the different treatments. Entry 7 had lower stem weight in both the artificially and naturally inoculated treatments when compared to the protected treatment. Stem dry weight of the other five entries were not modified by treatments. Entry by time of observation interaction was mainly due to the time at which entries reached their maximum stem weight. Stems of entry 1 had a maximal weight at the second sampling date. Entries 2, 3, 4, and 5 had higher stem dry weight between the third and fourth date. Entry 10 reached its maximum stem weight at the fifth sampling date.

Due to entries height differences, stem weight by unit of stem length was analyzed. Information on this variable is presented in Table 38. In addition to the factors and interactions which were significant for the variable stem dry weight, stem weight by unit of stem length showed significant differences among treatments. Protected plots had across sampling dates heavier stems by unit of length than

Table 37. Mean stem dry weight (g) at different sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated in 1985-86.

Sampling Treat. Date	Entry 1	3	4	5	7	10	Mean1/
Protec. 1	2.48	2.82	2.41	2.67	3.08	2.60	2.68
Nat. Inoc.	2.17	2.74	2.60	3.19	3.01	2.75	2.74
Artif. Inoc.	2.23	2.97	2.47	2.93	3.10	2.77	2.75
Mean 2/	2.29	2.84	2.49	2.93	3.06	2.71	
Protec. 2	2.80	3.21	2.75	3.25	3.40	2.97	3.06
Nat. Inoc.	2.79	3.31	2.94	3.06	2.71	2.55	2.89
Artif. Inoc.	2.78	2.92	2.64	3.08	2.90	2.73	2.84
Mean	2.79	3.15	2.78	3.13	3.00	2.75	
Protec. 3	2.37	2.98	2.39	3.56	3.19	3.21	2.95
Nat. Inoc.	2.55	2.79	3.15	3.48	2.62	3.08	2.95
Artif. Inoc.	2.59	2.82	2.84	3.31	2.50	3.55	2.94
Mean	2.50	2.86	2.80	3.45	2.77	3.28	
Protec. 4	2.42	3.27	3.08	3.70	2.75	3.34	3.09
Nat. Inoc.	2.15	3.40	2.97	3.65	3.21	3.14	3.09
Artif. Inoc.	2.39	2.85	2.77	3.66	2.83	3.54	3.01
Mean	2.32	3.17	2.94	3.67	2.93	3.34	
Protec. 5	1.87	2.94	2.47	3.62	3.11	3.83	2.97
Nat. Inoc.	1.84	2.81	2.85	3.48	2.80	3.66	2.91
Artif. Inoc.	2.01	2.87	2.82	3.34	2.90	4.01	2.99
Mean	1.90	2.87	2.71	3.48	2.93	3.83	
Protect. 6	1.91	2.69	2.32	3.18	2.89	3.08	2.68
Nat. Inoc.	1.64	2.39	2.55	3.00	2.19	3.19	2.49
Artif. Inoc.	1.65	2.48	2.69	2.80	2.39	3.35	2.56
Mean	1.73	2.52	2.52	2.99	2.49	3.21	
Protec. 7	1.66	2.65	2.01	2.47	2.64	2.98	2.40
Nat. Inoc.	1.68	2.19	2.10	2.23	1.93	2.35	2.08
Artif. inoc.	1.61	2.33	1.95	2.28	1.99	2.50	2.11
Mean	1.65	2.39	2.02	2.33	2.19	2.61	

Std. errors: 1/sampling date x treat.,0.07; 2/sampling date x entry, 0.10; sampling date x entry x treat., 0.18.

Table 38. Mean stem dry weight by unit of stem length (g/cm) at different sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated in 1985-86.

Sampling Treat. Date	Entry 1	3	4	5	7	10	Mean1/
Protec. 1	3.21	3.86	3.74	3.18	4.05	2.84	3.48
Nat. Inoc.	2.83	3.61	3.80	3.54	3.83	2.96	3.43
Artif. Inoc.	2.77	3.64	3.60	3.23	3.79	3.02	3.34
Mean 2/	2.93	3.71	3.71	3.32	3.89	2.94	
Protec. 2	2.80	3.21	2.75	3.25	3.40	2.97	3.06
Nat. Inoc.	2.79	3.31	2.94	3.06	2.71	2.55	2.89
Artif. Inoc.	2.78	2.92	2.64	3.08	2.90	2.73	2.84
Mean	2.79	3.15	2.78	3.13	3.00	2.75	
Protec. 3	2.97	3.14	2.64	3.49	3.30	2.89	3.07
Nat. Inoc.	3.00	2.91	3.17	3.33	2.63	2.72	2.96
Artif. Inoc.	3.03	2.97	2.88	3.09	2.51	3.13	2.93
Mean	3.00	3.00	2.90	3.30	2.81	2.91	
Protec. 4	2.93	3.44	3.25	3.66	2.81	3.04	3.19
Nat. Inoc.	2.54	3.48	2.99	3.39	2.98	2.81	3.03
Artif. Inoc.	2.82	2.88	2.85	3.41	2.65	3.12	2.95
Mean	2.77	3.27	3.03	3.48	2.81	2.99	
Protec. 5	2.31	3.07	2.69	3.40	3.17	3.43	3.01
Nat. Inoc.	2.15	2.79	2.95	3.29	2.71	3.15	2.84
Artif. Inoc.	2.34	2.90	2.84	3.18	2.73	3.57	2.93
Mean	2.27	2.92	2.82	3.29	2.87	3.38	
Protec. 6	2.33	2.78	2.41	2.96	2.77	2.80	2.67
Nat. inoc.	1.95	2.41	2.55	2.84	2.09	2.83	2.44
Artif. Inoc.	1.91	2.49	2.68	2.64	2.22	2.90	2.48
Mean	2.06	2.56	2.55	2.81	2.36	2.84	
Protec. 7	2.02	2.63	2.13	2.40	2.73	2.73	2.44
Nat. Inoc.	1.91	2.22	2.02	2.04	1.86	2.03	2.02
Artif. Inoc.	1.84	2.31	1.88	2.10	1.92	2.12	2.03
Mean	1.92	2.39	2.01	2.18	2.17	2.30	

Std. errors: 1/sampling date x treat.,0.07; 2/sampling date x entry, 0.10; sampling date x entry x treat., 0.17.

either inoculated treatments. Entries 1, 3, 5, and 7 showed a reduction in stem weight by unit of stem length between the protected and naturally inoculated treatment, while entry 4 reflected a slight increase between these two treatments. A reduction from the protected to the naturally inoculated treatment was found for entry 10, but stem weight by unit of stem length increased between the naturally and the artificially inoculated treatment. Entries 3, 4, and 7 had the highest stem weight by unit of length at the first sampling date. While entry 10 had the highest values at the fifth sampling date.

Spike dry weight analyzed at each sampling date produced heterogeneous error variances. Error mean squares increased in this variable according to increases of the experiment mean. Therefore, spike dry weight data were transformed using the log (x+1) equation, where log=logarithm base 10, and x=spike dry weight. After this variable was transformed, analysis of variances conducted at each sampling date had homogeneous error variances. Results found for spike dry weight are presented in Table 39. The combined analysis of dates indicated significant differences among treatments, entries, time of observation, interactions of treatment with entry, treatment with time of observation, and entry with time of observation. The interaction between entry and treatment was mainly the effect of the larger reduction in spike dry weight suffered by entries 3 and 7 from the protected to the naturally inoculated treatment. Entries 1, 5, and 10 had a more moderate reduction between these two treatments. While entry 4 increased spike dry weight from the protected to the naturally inoculated treatment. Only small changes were observed in spike dry

Table 39. Mean spike dry weight (g) at different sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated in 1985-86.

Sampling Treat. Date	Entry 1	3	4	5	7	10	Mean1/
Protec. 1	0.54	0.50	0.34	0.50	0.51	0.54	0.49
Nat. Inoc.	0.52	0.50	0.36	0.57	0.52	0.54	0.50
Artif.Inoc.	0.54	0.52	0.33	0.54	0.55	0.53	0.50
Mean 2/	0.53	0.51	0.34	0.54	0.53	0.53	
Protec. 2	0.53	0.64	0.50	0.50	0.64	0.54	0.56
Nat. Inoc.	0.51	0.66	0.57	0.57	0.50	0.54	0.56
Artif.Inoc.	0.56	0.64	0.52	0.54	0.57	0.53	0.56
Mean	0.53	0.65	0.53	0.54	0.57	0.53	
Protec. 3	1.01	1.06	0.78	0.89	0.93	0.85	0.92
Nat. Inoc.	1.03	1.04	1.06	0.93	0.73	0.80	0.94
Artif.Inoc.	1.08	1.06	0.88	0.85	0.69	0.87	0.91
Mean	1.04	1.05	0.91	0.89	0.78	0.86	
Protec. 4	1.77	1.72	1.41	1.33	1.30	1.41	1.49
Nat. Inoc.	1.61	1.77	1.34	1.38	1.50	1.31	1.48
Artif.Inoc.	1.84	1.44	1.32	1.35	1.31	1.55	1.47
Mean	1.74	1.64	1.36	1.36	1.37	1.43	
Protec. 5	2.18	2.05	1.57	2.05	2.31	1.89	2.01
Nat. Inoc.	2.21	2.01	1.74	2.14	1.94	2.08	2.02
Artif.Inoc.	2.28	2.01	1.82	1.95	2.07	1.84	2.00
Mean	2.22	2.02	1.71	2.05	2.11	1.94	
Protec. 6	2.81	3.23	2.36	2.54	2.89	2.56	2.73
Nat. Inoc.	2.75	2.45	2.57	2.44	2.48	2.78	2.58
Artif.Inoc.	2.80	2.80	2.64	2.58	2.55	2.90	2.71
Mean	2.79	2.82	2.52	2.52	2.64	2.74	
Protect. 7	3.49	4.14	3.08	3.74	4.17	3.25	3.65
Nat. Inoc.	3.16	2.91	2.98	3.49	3.00	2.62	3.03
Artif.Inoc.	3.09	3.08	3.07	3.62	3.04	2.88	3.13
Mean	3.25	3.38	3.05	3.61	3.41	2.92	

Std. errors: 1/sampling date x treat.,0.06; 2/sampling date x entry, 0.08; sampling date x entry x treat., 0.14.

weight of the different entries from the naturally inoculated compared to the artificially inoculated treatments. Treatment by time of observation interaction could be explained by the differences between protected and naturally inoculated treatments at sampling dates 1 and 7. All entries showed a steady spike dry weight increase from sampling date 1 to 7, although, changes between these dates were not equal for all entries. These different rates of spike dry weight increase contributed to the significance of the entry by time of observation interaction. Spike dry weight differences among treatments were observed only at sampling dates 1 and 7.

Dry weight of the top four leaves was measured twice during the grain filling period. This variable was not influenced by the treatments. Dry weight for the top four leaves obtained at the two sampling dates can be found in Table 40.

The advance of septoria tritici blotch to the flag leaf was studied by calculating the flag leaf disease progress coefficient (FLDPC). This coefficient was computed by dividing flag leaf diseased area by flag leaf total area. Disease progress coefficients on flag leaves obtained during six sampling dates are presented in Table 41. Analysis of variances conducted on this variable at each sampling date indicated heterogeneous error variances which increased as the experiment mean increased. Data were transformed using the log (x+1) equation and the analysis of the transformed data produced homogeneous error variances. Differences among treatments, entries, time of observations, and among all interactions were observed through the combined analysis of sampling dates. Septoria tritici blotch did not

Table 40. Mean dry weight of top four leaves (g) at two sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated in 1985-86.

Sampling Treat. Date	Entry 1	3	4	5	7	10	Mean 1/3/
Protec. 1	3.19	3.13	2.97	3.48	2.74	2.72	3.04
Nat. Inoc.	2.88	2.88	3.00	2.96	2.19	2.46	2.73
Artif. Inoc.	2.86	2.84	2.81	3.02	2.35	2.75	2.77
Mean 2/	2.98	2.95	2.93	3.15	2.43	2.64	
Protec. 2	1.96	2.23	2.28	2.39	1.90	2.17	2.16
Nat. Inoc.	2.22	2.12	2.40	2.35	2.04	2.08	2.20
Artif. Inoc.	1.94	2.01	2.41	2.26	1.95	1.99	2.09
Mean 4/	2.04	2.12	2.36	2.33	1.96	2.08	

Std. errors: First date: 1/ treatment, 0.08;
2/ entry, 0.09; entry x treat., 0.15.
Second date: 3/ treatment, 0.07;
4/ entry, 0.06; entry x treat., 0.11.

Table 41. Ratio between flag leaf diseased area and flag leaf total area at different sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated in 1985-86.

Sampling Treat. Date	Entry 1	3	4	5	7	10	Mean1/
Protec. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nat. Inoc.	0.00	0.15	0.00	0.01	0.10	0.00	0.04
Artif. Inoc.	0.00	0.26	0.00	0.00	0.09	0.00	0.06
Mean 2/	0.00	0.13	0.00	0.00	0.06	0.00	
Protec. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nat. Inoc.	0.00	0.15	0.00	0.00	0.12	0.00	0.04
Artif. Inoc.	0.00	0.42	0.00	0.01	0.3	0.01	0.12
Mean	0.00	0.19	0.00	0.00	0.14	0.00	
Protec. 3	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nat. Inoc.	0.00	0.21	0.00	0.01	0.13	0.08	0.07
Artif. Inoc.	0.02	0.26	0.00	0.02	0.33	0.04	0.11
Mean	0.01	0.16	0.00	0.01	0.16	0.04	
Protec. 4	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nat. Inoc.	0.03	0.37	0.04	0.01	0.60	0.10	0.19
Artif. Inoc.	0.17	0.66	0.13	0.06	0.45	0.11	0.27
Mean	0.06	0.35	0.06	0.03	0.35	0.07	
Protec. 5	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nat. Inoc.	0.10	0.75	0.05	0.21	0.52	0.08	0.28
Artif. Inoc.	0.40	0.80	0.23	0.37	0.87	0.43	0.53
Mean	0.17	0.54	0.09	0.19	0.46	0.17	
Protec. 6	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nat. Inoc.	0.48	0.99	0.15	0.19	1.00	0.37	0.53
Artif. Inoc.	0.76	1.00	0.28	0.42	1.00	0.44	0.65
Mean	0.42	0.66	0.14	0.20	0.67	0.27	

Std. errors: 1/sampling date x treat.,0.01; 2/sampling date x entry, 0.01; sampling date x entry x treat., 0.08.

develop in flag leaves of fungicide-protected plots. The disease progressed faster during the first four sampling dates on the flag leaves of artificially inoculated plots than it did in the naturally inoculated plots. No differences were detected between these two treatments during the last two sampling dates. On sampling date 6, flag leaves of artificially inoculated plots had an average of 65% of their area affected by septoria tritici blotch. Disease progress coefficients differ for entries throughout sampling dates. Entries 3 and 7, which had the highest rates of disease increase, were the most susceptible to the advance of the disease to the flag leaves. Entry 4 was the most resistant having a low rate of flag leaf disease progress. This entry had at the last sampling date in naturally as well as in artificially inoculated plots an average of 15 and 28% of the flag leaf area destroyed by septoria tritici blotch respectively. Entries 1, 5, and 10 had at the last sampling date FLDPC values between those of the resistant and susceptible entries. These entries resisted invasion by *S. tritici* up to the fourth sampling date, at which time they had the same affected flag leaf area as the resistant entries. During the last two sampling dates these entries suffered a high rate of disease advance to the flag leaves.

Correlations between FLDPC and six variables for sampling date 6 are presented in Table 42. The highest negative correlation was with FLDPC and the variable stem dry weight by unit of stem length ($r=-0.57$, $p<0.05$). Correlation coefficients with the other variables were negative and low.

Septoria tritici blotch severity were assessed by visual

Table 42. Coefficients of the correlation between flag disease progress coefficient at the 6th sampling date for entries in 1985-86 (N=18).

Stem dry weight (g)	-0.37
Stem dry weight (g/cm)	-0.57*
Spike dry weight (g)	-0.17
Plot grain yield (kg/ha)	-0.31
Number of seeds/spike	-0.15
1000 kernel weight (g)	-0.23

Coefficients followed by * are significantly different from "0" at the 0.05 probability level.

estimation of diseased leaf area and by measuring actual diseased area with a leaf area meter. Disease severity scores obtained by these two methods were compared. On the susceptible cultivars, Malcolm and Stephens, the visual assessment underestimated actual diseased area in naturally and artificially inoculated plots by 6 and 2% respectively. In the other entries the visual method overestimated actual flag leaves diseased area in naturally and artificially inoculated plots by an average of 17%. The average for the six entries in all inoculated plots was an overestimation of the actual disease severity levels by 10.65%. The correlation between both methods of disease estimation was high ($r=0.93$, $p<0.001$, $N=54$). The lowest correlation was found for entry 4 ($r=0.87$) and the highest in entries 3 and 7 ($r=1$).

Analysis of variances carried at each sampling date for the variables dry stems monosaccharide and disaccharide content had homogeneous error variances. The combined analysis of sampling dates for these variables indicated significant differences among treatments, entries, time of observation, and among all interactions. Dry stem monosaccharide content found in the different entries through sampling dates are presented in Table 43. Differences among treatments were significant during sampling dates 1, 5, 6, and 7. At the fifth sampling date, the artificially inoculated plots had higher monosaccharide content than the naturally inoculated plots. During the last two sampling dates, the protected treatment had a higher dry stem monosaccharide content than either of the inoculated treatments. Although differences were found among entries at each sampling date, it was at the sixth and seventh dates where maximized differences among

Table 43. Mean dry stem monosaccharide content (mg/g dry stem) at different sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated in 1985-86.

Sampling Treat. Date	Entry 1	3	4	5	7	10	Mean1/
Protec 1	23.52	35.76	73.83	17.30	55.92	40.53	41.14
Nat. Inoc.	24.69	25.96	57.73	26.30	44.59	52.39	38.61
Artif.Inoc.	24.91	22.95	56.86	17.28	38.71	54.97	35.95
Mean 2/	24.37	28.22	62.81	20.29	46.40	49.30	
Protec. 2	26.45	34.36	63.87	35.45	37.48	56.40	42.33
Nat. Inoc.	27.09	26.41	57.22	27.71	37.18	50.37	37.66
Artif.Inoc.	28.32	27.61	58.26	32.41	37.29	55.12	39.84
Mean	27.29	29.46	59.78	31.86	37.32	53.96	
Protec. 3	31.11	35.58	48.38	23.88	48.56	47.28	39.13
Nat. Inoc.	33.40	41.35	47.36	24.72	45.49	55.00	41.22
Artif.Inoc.	34.09	40.39	44.51	30.86	41.97	48.14	39.99
Mean	32.87	39.10	46.75	26.48	45.34	50.14	
Protec. 4	47.02	39.24	53.67	33.45	41.43	41.65	42.74
Nat. Inoc.	58.53	44.87	45.02	39.07	50.69	43.96	47.02
Artif.Inoc.	57.28	41.11	52.56	35.60	43.15	37.14	44.47
Mean	54.28	41.74	50.42	36.04	45.09	40.91	
Protec. 5	42.08	35.92	44.92	42.27	38.35	39.22	40.46
Nat. Inoc.	45.56	39.85	39.84	38.73	48.26	39.83	42.01
Artif.Inoc.	46.16	41.10	45.92	38.91	61.50	49.67	47.21
Mean	44.60	38.96	43.56	39.97	49.37	42.91	
Protec. 6	62.15	49.42	90.84	86.58	64.41	81.38	72.64
Nat. Inoc.	50.80	48.41	83.91	90.99	56.87	66.26	66.20
Artif.Inoc.	34.98	26.52	88.57	83.33	38.12	69.10	56.77
Mean	49.31	41.45	87.77	86.96	53.13	72.24	
Protec. 7	10.75	7.59	54.44	49.54	30.87	97.60	41.80
Nat. Inoc.	8.86	3.50	45.57	32.36	7.07	54.78	25.36
Artif.Inoc.	9.61	3.08	30.28	18.37	5.60	63.19	21.69
Mean	9.74	4.72	43.43	33.42	14.51	71.86	

Std. errors: 1/sampling date x treat.,0.78; 2/sampling date x entry, 1.10; sampling date x entry x treat., 1.90.

entries were found. At sampling date 6 entries 4 and 5 had the highest levels of dry stem monosaccharides. Entries 1, 3, and 7 had the lowest levels at the sixth and also at the last sampling date. At this last sampling date, entry 10 had the highest dry stem monosaccharide levels, while entries 4 and 5 had intermediate values. Entries 1, 7, and 10 had at the sixth sampling date higher dry stem monosaccharide levels in protected plots than in either the natural or artificial inoculated plots. In contrast with what was found in other entries, entries 1 and 3 had at the last sampling date small differences in dry stem monosaccharide content between the protected and inoculated treatments.

A similar pattern noted for monosaccharides was also observed for dry stem disaccharide content. Values observed for dry stem disaccharide content for the six entries can be found in Table 44. Differences among treatments were the greatest on sampling dates 6 and 7. No differences were observed between the two inoculated treatments at the last sampling date. Maximized differences at sampling date 6 were noted for all entries. Entry 4 had the highest levels throughout the experiment followed by entries 10 and 5 at the sixth date. At the lower end of the rankings were entries 1, 3, and 7. Entries 7 and 10 showed at the sixth sampling date a larger disaccharide content in the protected than in either of the inoculated treatments. At the same sampling date, entries 1 and 3 had more disaccharides in the protected and naturally inoculated treatments than in the artificial inoculated plots. Entries 4 and 5 did not show differences among treatments at any sampling date.

Dry stem monosaccharide and disaccharide content of entries

Table 44. Mean dry stem disaccharide content (mg/g dry stem) at different sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated in 1985-86.

Sampling Treat. Date	Entry 1	3	4	5	7	10	Mean 1/
Protec. 1	30.04	21.29	30.57	19.19	21.27	30.77	25.52
Nat. Inoc.	25.47	21.39	28.51	24.82	19.90	25.33	24.24
Artif.Inoc.	22.50	23.93	23.96	19.05	22.88	29.59	23.66
Mean 2/	26.02	22.20	27.68	21.02	21.35	28.56	
Protec. 2	24.76	25.07	30.07	25.43	22.70	24.58	25.40
Nat. Inoc.	26.09	25.59	33.83	26.04	23.15	23.67	26.39
Artif.Inoc.	28.19	26.22	32.78	22.81	20.46	25.45	25.99
Mean	26.35	25.62	32.23	24.76	22.10	24.57	
Protec. 3	27.81	36.30	40.37	25.74	21.57	26.81	29.77
Nat. Inoc.	28.24	29.59	40.95	25.02	23.91	22.80	28.42
Artif.Inoc.	27.86	29.21	44.76	27.80	21.90	29.18	30.12
Mean	27.97	31.70	42.02	26.19	22.46	26.27	
Protec. 4	31.40	37.24	40.95	27.88	30.89	36.58	34.16
Nat. Inoc.	33.20	35.18	41.62	27.14	26.49	36.88	33.42
Artif.Inoc.	32.52	35.61	44.24	28.84	29.57	35.77	34.42
Mean	32.39	36.01	42.27	27.95	28.98	36.41	
Protec. 5	29.51	29.29	41.01	29.64	24.53	34.59	31.43
Nat. Inoc.	24.44	30.65	38.13	27.10	21.14	29.05	28.42
Artif.Inoc.	27.23	31.22	34.80	27.26	24.85	35.22	30.10
Mean	27.06	30.38	37.98	28.00	23.51	32.96	
Protec. 6	20.73	22.71	58.82	36.25	28.60	56.80	37.32
Nat. Inoc.	20.66	22.00	59.10	34.14	17.53	41.22	32.44
Artif.Inoc.	7.60	8.20	65.47	29.92	12.54	45.37	28.18
Mean	16.33	17.64	61.13	33.44	19.56	47.80	
Protec. 7	0.97	4.10	14.30	12.90	3.07	9.60	7.49
Nat. Inoc.	0.67	1.00	15.35	4.91	1.83	3.93	4.62
Artif.Inoc.	1.16	0.71	9.44	5.92	0.90	4.76	3.83
Mean	0.94	1.94	13.03	7.91	1.95	6.10	

Std. errors: 1/sampling date x treat.,0.56; 2/sampling date x entry, 0.79; sampling date x entry x treat., 1.36.

averaged across sampling dates are presented in Table 45. This table presents also the amount of these saccharides lost in the inoculated treatments compared with the protected treatment. Entries 4, 7, and 10 suffered the highest monosaccharide loss in the naturally inoculated treatment. For the artificially inoculated treatment all entries suffered monosaccharide losses, although entries 1 and 10 had the least. Only entries 7 and 10 lost large amount of disaccharides in the naturally inoculated treatment. For the artificially inoculated treatment all entries, with the exception of 4, suffered losses.

Analysis of variances carried out for each sampling date involving the variables phloem exudate monosaccharide and disaccharide content, extracted either from flag leaves or stems, had heterogeneous error variances. No relationship was found between error means squares and the means of each sampling date. Consequently, the combined analysis of sampling dates was not performed for these variables.

The level of monosaccharides measured in flag leaf phloem exudate was not affected by treatments at any sampling date. Entries differed in the amount of monosaccharides collected in flag leaf exudate during the first four sampling dates. Entries 5, 7, and 10 maintained a higher monosaccharide level throughout most sampling dates than the other three entries. Table 46 describes monosaccharide levels found on flag leaf phloem exudate at each sampling date for each entry.

The amount of disaccharides measured on flag leaf phloem exudate was also not affected by treatments, with the exception found at sampling date 4. At this date, the protected treatment was different from the artificially inoculated treatment. Differences among entries

Table 45. Mean dry stem total monosaccharide and disaccharide content (mg/g dry stem) averaged across sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated in 1985-86.

Entry	Treatment				
	Protec.	Nat. Inoculat.		Artif. Inoculat.	
	Monosaccharide				
1	34.63	35.56	(+ 2.4)	33.62	(- 3.2)
3	33.98	32.91	(- 3.2)	28.97	(-14.8)
4	61.42	53.81	(-12.4)	53.85	(-12.3)
5	41.21	39.98	(- 3.0)	36.68	(-11.0)
7	45.29	41.45	(- 8.5)	38.05	(-16.0)
10	57.72	51.80	(-10.3)	53.90	(- 6.6)
Mean 1/	45.73	42.58	(- 7.0)	40.85	(-10.7)
	Disaccharide				
1	23.61	22.68	(- 3.9)	21.02	(-11.0)
3	25.14	23.63	(- 6.0)	22.16	(-11.9)
4	36.58	36.78	(+ 0.5)	36.49	(- 0.3)
5	25.29	24.17	(- 4.4)	23.09	(- 8.7)
7	21.81	19.14	(-12.2)	19.02	(-12.8)
10	31.39	26.13	(-16.8)	29.33	(- 6.6)
Mean 2/	27.30	25.42	(- 6.9)	25.18	(- 7.8)

Figure between parenthesis indicates percent difference from the protected treatment.
Std. error: 1/ treatment, 0.54; entry x treat., 0.57.
2/ treatment, 0.13; entry x treat., 0.50.

Table 46. Mean flag leaf phloem exudate monosaccharide content (mg/leaf) at different sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated in 1985-86.

Sampling Treat. Date	Entry 1	3	4	5	7	10	Mean1/
Protec. 1	2.76	2.55	2.96	4.30	7.56	2.99	3.85
Nat. Inoc.	4.09	2.94	2.68	4.74	10.15	4.70	4.89
Artif.Inoc.	4.38	3.02	3.10	5.40	5.38	3.83	4.18
Mean 2/	3.74	2.84	2.91	4.81	7.70	3.84	
Protec. 2	6.79	4.00	3.24	3.54	5.31	7.54	5.07
Nat. Inoc.	7.52	5.82	5.68	6.28	5.73	13.16	7.37
Artif.Inoc.	0.70	5.68	5.15	5.02	4.07	9.15	6.63
Mean	8.34	5.17	4.69	4.95	5.03	9.95	
Protec. 3	4.44	4.56	5.65	6.07	7.25	11.25	6.54
Nat. Inoc.	6.49	5.23	6.17	8.91	7.46	10.34	7.43
Artif.Inoc.	6.81	5.80	5.25	8.02	6.29	13.81	7.66
Mean	5.91	5.20	5.69	7.67	7.00	11.80	
Protec. 4	3.91	5.08	4.69	5.73	7.39	8.69	5.92
Nat. Inoc.	4.69	4.80	7.18	8.04	6.50	8.22	6.57
Artif.Inoc.	4.69	4.45	8.77	12.08	6.06	5.17	6.87
Mean	4.43	4.77	6.88	8.62	6.65	7.36	
Protec. 5	7.85	4.46	4.58	8.01	8.01	4.89	6.30
Nat. Inoc.	5.63	5.89	6.82	5.14	6.49	5.95	5.99
Artif.Inoc.	5.87	4.31	5.21	6.05	5.63	4.95	5.34
Mean	6.45	4.89	5.53	6.40	6.71	5.26	
Protec. 6	8.40	4.53	6.52	5.78	12.52	6.16	7.32
Nat. Inoc.	8.70	5.98	9.02	9.98	11.47	11.13	9.38
Artif.Inoc.	0.84	3.82	10.16	7.64	7.65	10.54	8.44
Mean	9.31	4.78	8.57	7.80	10.55	9.28	

Std. errors: Date 1: treat., 0.35; entry, 0.91; treat. x entry, 1.58.
Date 2: treat., 0.55; entry, 0.99; treat. x entry, 1.71.
Date 3: treat., 0.45; entry, 0.57; treat. x entry, 0.98.
Date 4: treat., 0.32; entry, 0.59; treat. x entry, 1.02.
Date 5: treat., 0.25; entry, 0.66; treat. x entry, 1.15.
Date 6: treat., 0.79; entry, 1.31; treat. x entry, 2.28.

were found at each sampling date with the exception of date 3. Disaccharide levels found on flag leaf phloem exudate at each sampling date can be found in Table 47.

Analyses were also conducted on flag leaf monosaccharide and disaccharide content expressed by unit of flag leaf area. Values found for monosaccharide and disaccharide content in flag leaf exudate by cm^2 of flag leaf are presented in Table 48. As it was the case for flag leaf phloem saccharides levels in whole leaves, monosaccharide and disaccharide levels by unit of leaf area were not affected by treatments. Entry 7 had the highest levels of flag leaf phloem monosaccharides and disaccharides throughout most sampling dates while entry 1 had the lowest levels.

The total monosaccharide and disaccharide content of stem phloem exudate was higher for the protected than for either of the inoculated treatments throughout the experiment. However, significant differences were only demonstrated at sampling dates 2, 4, and 5. Entries differed in the total monosaccharide and disaccharide content collected in stems phloem exudate, although, there it was no consistent classification of entries at the various sampling dates. Monosaccharide and disaccharide levels found on stem phloem exudate can be found in Table 49.

Correlations between monosaccharide and disaccharide content either in flag leaf or stem phloem exudate or in dry stems with several variables are presented in Table 50. Flag leaf total monosaccharide and disaccharide measured in phloem exudate had the highest positive correlation with stem dry weight. The same variable was negatively correlated with spike dry weight. All other correlation coefficients

Table 47. Mean flag leaf phloem exudate disaccharide content (mg/leaf) at different sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated in 1985-86.

Sampling Treat. Date	Entry 1	3	4	5	7	10	Mean
Protec. 1	5.94	9.56	19.04	11.33	31.04	17.85	15.80
Nat. Inoc.	4.84	7.57	12.53	9.84	28.08	25.58	14.74
Artif.Inoc.	8.28	8.03	13.05	11.49	16.89	31.85	14.93
Mean	6.36	8.39	14.87	10.89	25.34	25.09	
Protec. 2	4.09	3.10	3.17	11.50	8.31	5.54	5.95
Nat. Inoc.	3.33	3.30	5.10	17.68	6.94	3.98	6.72
Artif.Inoc.	4.81	4.44	5.10	10.28	3.55	8.57	6.13
Mean	4.08	3.62	4.46	13.15	6.27	6.03	
Protec. 3	3.26	3.23	3.44	3.48	3.49	3.04	3.32
Nat. Inoc.	3.35	3.04	3.27	3.49	3.32	2.95	3.24
Artif.Inoc.	3.04	2.93	3.33	3.56	2.84	3.56	3.21
Mean	3.22	3.07	3.35	3.51	3.22	3.19	
Protec. 4	3.05	3.70	3.50	3.53	3.47	3.29	3.42
Nat. Inoc.	3.18	2.95	3.24	3.17	3.03	3.5	3.18
Artif.Inoc.	3.08	3.04	3.27	3.73	3.16	1.18	2.91
Mean	3.10	3.23	3.33	3.48	3.22	2.66	
Protec. 5	3.46	3.28	3.71	3.29	4.04	2.30	3.34
Nat. Inoc.	0.00	2.92	2.98	3.08	3.09	2.24	2.38
Artif.Inoc.	0.00	3.19	3.15	2.84	3.38	1.70	2.38
Mean	1.15	3.13	3.28	3.07	3.51	2.08	
Protect. 6	0.00	3.47	5.26	4.71	4.18	3.46	3.51
Nat. Inoc.	0.00	4.41	3.24	3.51	3.83	0.00	2.50
Artif.Inoc.	1.57	3.61	3.49	4.25	4.14	3.25	3.38
Mean	0.52	3.83	4.00	4.16	4.05	2.24	

Std. errors: Date 1: treat., 1.19; entry, 2.69; treat. x entry, 4.66.
Date 2: treat., 0.55; entry, 0.94; treat. x entry, 1.62.
Date 3: treat., 0.13; entry, 0.11; treat. x entry, 0.19.
Date 4: treat., 0.09; entry, 0.15; treat. x entry, 0.26.
Date 5: treat., 0.23; entry, 0.25; treat. x entry, 0.44.
Date 6: treat., 0.30; entry, 0.27; treat. x entry, 0.47.

Table 48. Mean flag leaf phloem exudate total monosaccharide and disaccharide content by unit of flag leaf area (mg/cm^2) at different sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated in 1985-86.

Sampling Treat. Date	Entry 1	3	4	5	7	10	Mean
Protec. 1	0.26	0.47	0.70	0.45	1.33	0.56	0.63
Nat. Inoc.	0.26	0.48	0.61	0.42	1.50	0.80	0.68
Artif.Inoc.	0.36	0.33	0.62	0.50	0.66	0.90	0.56
Mean	0.29	0.43	0.64	0.46	1.17	0.75	
Protec. 2	0.22	0.16	0.16	0.28	0.44	0.31	0.26
Nat. Inoc.	0.22	0.25	0.26	0.52	0.42	0.52	0.36
Artif.Inoc.	0.31	0.24	0.28	0.29	0.24	0.45	0.30
Mean	0.25	0.22	0.23	0.37	0.37	0.43	
Protec. 3	0.17	0.19	0.22	0.18	0.26	0.30	0.22
Nat. Inoc.	0.25	0.25	0.23	0.27	0.27	0.31	0.26
Artif.Inoc.	0.23	0.23	0.20	0.26	0.20	0.32	0.24
Mean	0.22	0.22	0.22	0.24	0.24	0.31	
Protec. 4	0.13	0.20	0.20	0.18	0.34	0.30	0.22
Nat. Inoc.	0.14	0.22	0.25	0.21	0.30	0.28	0.23
Artif.Inoc.	0.15	0.21	0.26	0.33	0.27	0.11	0.22
Mean	0.14	0.21	0.24	0.24	0.30	0.23	
Protec. 5	0.21	0.16	0.18	0.23	0.29	0.13	0.20
Nat. Inoc.	0.12	0.30	0.21	0.16	0.30	0.16	0.21
Artif.Inoc.	0.13	0.23	0.17	0.19	0.33	0.14	0.19
Mean	0.15	0.23	0.19	0.19	0.30	0.14	
Protec. 6	0.18	0.21	0.31	0.26	0.63	0.23	0.30
Nat. Inoc.	0.20	0.32	0.33	0.32	0.57	0.27	0.34
Artif.Inoc.	0.31	0.22	0.33	0.25	0.40	0.38	0.32
Mean	0.23	0.25	0.32	0.28	0.53	0.29	

Std. errors: Date 1: treat., 0.04; entry, 0.12; treat. x entry, 0.21.
Date 2: treat., 0.02; entry, 0.03; treat. x entry, 0.06.
Date 3: treat., 0.01; entry, 0.02; treat. x entry, 0.03.
Date 4: treat., 0.008; entry, 0.02; treat. x entry, 0.03.
Date 5: treat., 0.007; entry, 0.02; treat. x entry, 0.03.
Date 6: treat., 0.02; entry, 0.05; treat. x entry, 0.08.

Table 49. Mean stem phloem exudate total monosaccharide and disaccharide content (mg/cm) at different sampling dates of entries either protected with fungicide or *Septoria tritici* inoculated in 1985-86.

Sampling Treat. Date	Entry 1	3	4	5	7	10	Mean
Protec. 1	0.42	0.79	1.79	0.65	0.74	1.36	0.96
Nat. Inoc.	0.42	0.82	1.41	0.46	0.57	1.46	0.86
Artif.Inoc.	0.43	0.63	1.86	0.85	0.62	1.29	0.95
Mean	0.42	0.74b	1.69	0.66	0.64	1.37	
Protec. 2	0.89	0.93	1.29	0.99	2.72	0.74	1.26
Nat. Inoc.	0.71	0.91	0.99	0.80	1.40	0.82	0.94
Artif.Inoc.	0.59	0.65	1.06	0.61	0.69	0.89	0.75
Mean	0.73	0.83	1.11	0.80	1.60	0.82	
Protec. 3	0.81	0.76	0.50	0.71	0.64	0.46	0.65
Nat. Inoc.	0.78	0.42	0.41	0.75	0.58	0.37	0.55
Artif.Inoc.	0.74	0.34	0.38	0.68	0.51	0.57	0.54
Mean	0.78	0.51	0.43	0.72	0.57	0.47	
Protec. 4	1.12	0.90	0.58	0.77	0.76	0.88	0.84
Nat. Inoc.	0.88	0.48	0.60	0.76	0.63	0.51	0.64
Artif.Inoc.	1.13	0.46	0.59	0.66	0.55	0.49	0.65
Mean	1.05	0.61	0.59	0.73	0.65	0.63	
Protec. 5	0.86	0.62	0.64	0.77	0.95	0.35	0.70
Nat. Inoc.	0.79	0.48	0.50	0.51	0.74	0.40	0.57
Artif.Inoc.	0.78	0.52	0.46	0.56	0.52	0.50	0.56
Mean	0.81	0.54	0.53	0.61	0.73	0.42	
Protec. 6	1.39	0.94	1.28	1.30	0.84	1.09	1.14
Nat. Inoc.	0.91	0.72	1.62	1.02	0.72	0.74	0.95
Artif.Inoc.	0.92	0.65	1.20	0.70	0.58	0.65	0.78
Mean	1.07	0.77	1.37	1.00	0.71	0.82	

Std. errors: Date 1: treat., 0.13; entry, 0.18; treat. x entry, 0.31.
Date 2: treat., 0.03; entry, 0.12; treat. x entry, 0.21.
Date 3: treat., 0.03; entry, 0.05; treat. x entry, 0.09.
Date 4: treat., 0.04; entry, 0.08; treat. x entry, 0.13.
Date 5: treat., 0.03; entry, 0.05; treat. x entry, 0.08.
Date 6: treat., 0.08; entry, 0.13; treat. x entry, 0.22.

involving flag leaf phloem exudate were positive and low, with the exception of that with FLDPC. Monosaccharides and disaccharides collected from stem phloem exudate were also negatively correlated with FLDPC. A significant positive correlation was found between monosaccharides and disaccharides collected from stem phloem exudate and spike dry weight, plot grain yield, and number of seeds per spike. Dry stem monosaccharides and disaccharides were also negatively correlated with FLDPC. Significant positive correlations were found between dry stem monosaccharide and disaccharide content and stem dry weight or stem dry weight per unit of stem length. Correlation coefficients between FLDPC and dry stem monosaccharide and disaccharide content calculated at sampling date 6 for each entry are presented in Table 51. With the exception of entries 3 and 4, all others entries had significant correlations between FLDPC and dry stem monosaccharide and disaccharide content. The resistant entry 4 had a positive, although not significant correlation between these two variables.

Table 50. Correlation coefficients of flag leaf and stem monosaccharide and disaccharide of entries in 1985-86 (N=18).

	Total phloem exudate mono and disaccharides		Dry stem	
	Flag leaf	Stem	monosacch.	disacch.
Flag leaf disease progress index	-0.24 (4)	-0.68** (6)	-0.70** (6)	-0.60** (6)
Stem weight (g)	0.61** (3)	0.15 (2)	0.52* (6)	0.51* (6)
Stem weight (g/cm)	0.16 (5)	0.46 (3)	0.57* (6)	0.54* (6)
Spike weight (g)	-0.62** (4)	0.53* (4)	0.36 (4)	0.25 (3)
Plot yield (kg/ha)	0.35 (5)	0.64** (5)	0.26 (4)	0.25 (3)
Number of seeds/spike	0.32 (5)	0.54* (6)	0.29 (4)	0.62** (3)

Coefficients followed by * or ** are significantly different from "0" at the 0.05 or 0.01 probability levels respectively.
() indicates sampling date at which the correlation was calculated.

Table 51. Correlation coefficients between flag leaf disease progress coefficient and total dry stem mono and disaccharides calculated at the 6th sampling date in entries in 1985-86 (N=9).

Entry	r
1	- 0.89**
3	- 0.53
4	0.27
5	- 0.74**
7	- 0.82**
10	- 0.82**

Coefficients followed by * or ** are significantly different from "0" at the 0.05 or 0.01 probability levels respectively.

DISCUSSION

The experimental plant materials for this study were selected based on their visual expression of symptoms to septoria tritici blotch when grown under field conditions in previous years. Thus a range of entries were available representing from susceptible to what appeared to be resistant disease reaction.

Controlled Environment Experiment

To study the effect of different amounts of superimposed *Septoria tritici* inoculations on selected winter wheat entries, controlled environmental conditions were employed. The experiment also provided an opportunity to test a moist inoculation chamber system especially designed for this study. This system performed well during the time the experiment was conducted by allowing optimal conditions for *Septoria tritici* infection and symptoms development.

Disease Reaction

Inoculum of *S. tritici* was applied at different stages of development, consequently, disease development was not only a function of susceptibility or resistance but also was influenced by the time inoculum was placed on the plants. This condition more closely resembles what occurs under field situations when entries are being evaluated under field environment, the inoculum may come at the same time regardless of the phenologic stage of the plants. Since entries used in this study were inoculated at the same time and they differed in maturity cycle, they received inoculum at different stages of development. Therefore, early entries received most of the

inoculations in a period of time from the beginning of flag leaf emergence to maturity. While later maturing entries were inoculated from the beginning of stem elongation to maturity or over a longer duration of plant development. This situation may have produced a differential effect of the disease according to host maturity cycle and resulted in a greater destruction of important plant parts such as flag leaves. The effect of inoculation at different growing stages is demonstrated by the presence of necrotic tissues in flag leaves of entries 1, 12, and 13. These necrotic tissues in the treatment that received only one inoculation, indicate that the flag leaf had already emerged at the time of that inoculation. Flag leaves of entries 6 and 10 appeared later than those of the other entries. Therefore, they were exposed to less inoculum, a condition that was manifested by the lower amount of necrotic tissues present in these plants in the treatment that received one inoculation. Nevertheless, resistance to septoria tritici blotch may have also played a role in interfering with disease development since entries 7 and 11, which were also late maturing, showed a high percent of flag leaf damage. Disease traces found in the flag and in the four top leaves of entry 13 in the noninoculated treatment could have been the result of contaminant inoculum or the effect of some other agent which was not possible to distinguish from Septoria.

Six inoculations caused disease development even in the resistant entry 6. This entry could still be distinguished from susceptible entries by comparing disease severity scores on either flag or four top leaves levels. Susceptible entry 12 developed high levels of disease

severity when receiving just one inoculation. This entry was severely affected by six inoculations, as it were less susceptible entries 1 and 13. Therefore, it seemed that six inoculations were excessive and overrode the resistant sources present. Three inoculations appeared to be enough to distinguish between susceptible, such as entry 12, and resistant, such as entries 6 and 10, or intermediate reactions like 1 and 13.

Entries can be separated into two groups based on heading dates. Entries 1, 12, and 13, were early while entries 6, 7, 10, and 12 were approximately 32 days later. The earliest heading entries were more affected by septoria tritici blotch. The extent of the correlation between days to heading and disease severity of the top four leaves ($r=-0.60$) confirms that there it was a tendency for late heading entries to have less disease. Due to the small number of entries studied, this relationship may only represent a fortuitous association of the experimental materials chosen.

The changes in disease severity observed with different number of inoculations were described by the regression coefficient of disease severity versus treatment. Susceptible entries such as 12 and 13 showed the largest absolute coefficients while resistant entries such as 6 and 10 had the smallest values. The sharp slope of the regression lines did indicate large differences in disease severity between the control and the inoculated plants. However, the regression coefficient did not provide any indication of the average disease severity suffered by each entry. Two entries with similar slopes may differ widely in the amount of disease they supported. Therefore, this coefficient is

most useful when provided with an indication of the disease severity based on the average treatment.

Effects on 1000 Kernel Weight and Number of Seeds per Spike

The effect of the number of inoculations on yield and the components of yield can be better evaluated when compared to losses suffered by the control. Kernel weight was less affected by the disease than was the number of seeds per spike. Most of the entries studied suffered seed losses after receiving three inoculations. These results confirm reports published by Lim and Gaunt (1978). They observed that Septoria infection before anthesis reduced the number of seeds per spike more than it did with 1000 kernel weight. Similar results were observed in selected genotypes by Scharen (personal communication) in the "Wheat Septoria Nursery" grown in Montana. As reported by Lim and Gaunt (1978) Septoria could have affected apical components such as total floret number, floret development, and floret death, all of which are reflected in a reduction in the number of grains per spike.

Effects on Tillering

The number of fertile tillers per plant was also important in determining yield differences among entries. A range of 4.52 was noted between the entries having the highest and lowest tiller count. Some fertile tillers were lost after receiving only one or two inoculations in entries such as 10 and 11. However, the largest reduction in tiller number was observed for all entries after receiving six inoculations.

The reduction in the number of fertile tillers per plant was important in decreasing total plant yield in most entries in treatments receiving three or six inoculations. This effect has seldom been reported as a significant cause of yield reduction by *S. tritici*. Harrower (1978) reported a reduction in the number of tillers in two out of the three wheat cultivars when inoculated at the seedling stage. Under field conditions Camacho-Casas (1986) observed a reduction in the number of fertile spikes due mainly to septoria tritici blotch. However, this effect was only seen when the soil had been fumigated to remove confounding factors due to root rot complexes.

In the present experiment data on tillering were collected ten days after the first inoculation. At this time growth stages of entries ranged from pseudo-stem elongation (Feekes's stage 5) to the time when the second node and last leaf were just visible (Feekes's stage 7 and 8). Tillering would normally be expected to be completed by stages 7 and 8. A this time, tiller number was not affected by treatments, but differences among entries were observed. However, at maturity a difference due to treatments was found for tiller number. The tiller number difference between the first observation and spikes counted at maturity may have been due to *S. tritici* precluding tillers to develop spikes or, alternatively, by inducing plants to differentially develop late spike-bearing tillers. To elucidate these alternatives the percentage of tillers counted at tillering stage to the number of tillers that developed spikes at maturity was calculated. Although all entries initiated new tillers after the initial tillering data were recorded, late tiller production was influenced by the number

of inoculations. Plants receiving none, to three inoculations developed approximately twofold more tillers than the initial count. Plants receiving six inoculations produced only 30% more new spike-bearing tillers. These data suggest that *S. tritici* affected plant yield by decreasing the production of late tillers rather than by killing or sterilizing earlier developed tillers. This effect may not be as important under field conditions. Scarcity of nutrients and moisture, increasing shading, and competition for space, could effectively limit the development of late tillers under field conditions. In the greenhouse most of these constraints were minimized and, therefore, plants realized some yield in late developed spikes. Data on individual spikes were not recorded and therefore comparisons among early and late developing spikes could not be made. With the high average kernel weight and number of seeds per spike recorded by entries it appears they contributed substantially to total plant yield under greenhouse conditions. There was no indication that late tillers decreased the average plant kernel weight or the number of seeds per spike which could happen as a compensatory mechanism when source-sink relationships were modified.

Effects on Grain Yield per Plant

Reduction in the yield of entries was realized with increasing number of inoculations. However, some entries were more affected than others in levels of yield reduction. The cultivar Stephens (entry 7) was the most affected as revealed by the sharp yield decline observed from the control to the treatment where six inoculations were applied.

The slope of the line describing yield decline provides an idea of the sensitivity of cultivars to increased amount of disease. It does not however provide a full characterization of the cultivar resistance. Stephens, and entries 6 and 10 were the most sensitive but they also had the highest plant mean yield. Stephens had higher yield than any other entry at all treatment levels with the exception for the treatment with six inoculations. Entry 12 had the most stable yield throughout the inoculation treatments, although, its mean plant yield was the lowest.

Correlations Between Disease Severity and Yield

The extent of the correlation between disease severity and yield may provide a rough estimate as to how yield is affected by increasing disease severity levels. In susceptible genotypes yield is normally negatively associated with disease severity. A weak correlation or lack of correlation may suggest that yield is not decreased to the same degree as the disease increase, a situation that describes disease tolerance. The analysis of the correlations between yield components and disease severity also may reveal genotypes that can compensate through a modification of the yield components. Disease severity measured for the top four leaves generally had higher correlation with yield than did the same association with the flag leaf. Thus the former coefficient seems to be the most adequate in describing disease severity-yield interactions. Regardless of the way in which the coefficients were calculated, the cultivar Yamhill (entry 11) appeared as the most tolerant. This cultivar suffered yield losses after

receiving two inoculations; however, it was not affected to any greater degree by higher numbers of inoculations. This cultivar tolerated disease mainly by sustaining a high number of spikes per plant despite the presence of high disease severity levels.

Greenhouse Screening for Disease Reaction

Sources of resistance to septoria tritici blotch can be identified under the controlled conditions of the greenhouse. Genotypes differing in maturity cycle could be inoculated at the same growth stage. However, this may involve the growth and inoculation of one genotype at a time or the inclusion in the screening of only genotypes having the same cycle. Alternatively, plants can be moved into the inoculation chambers only for the short period required for inoculation. This may impose logistic problems such as space availability and movement of plants around the facilities.

Assessment of disease severity using the top four leaves gave a better resolution of the disease reaction spectrum than did the flag leaf of the plant material used.

Field Experiments

Plant growth and disease development were affected during 1984-85 and 1985-86 growing season by the prevailing weather conditions. First growing season in which the experiment was conducted could be characterized as being too dry for disease development. While the second season was good for both wheat growth and for septoria tritici blotch development. Therefore, all variables measured reflected this

situation. Unpredictable variation in environmental conditions from year to year is one of the major problems breeders encounter in applying disease pressures to segregating populations to identify resistant progeny.

Effects of Natural and Artificial Inoculations on Disease Reaction

This field experiment was designed to measure the effects of natural and artificial *Septoria tritici* inoculations on wheat (Study 2). Unfortunately, little disease developed during the 1984-85 growing season. Disease levels obtained did allow for the identification of one susceptible cultivar (Stephens) and one resistant entry (6). Other entries showed no or little differences in disease reaction. Disease severity was assessed at the flag and at the top four leaves. Disease severity of the top four leaf during the 1984-85 cycle resulted in the largest differences between resistant and susceptible entries. The correlations between disease severity of the flag leaf and of the top four leaves were higher for the 1985-86 season (0.96, N=30) than for the 1984-85 growing season (0.86, N=30). In unfavorable years for Septoria development, due to the path followed by the disease from the basal to the upper leaves, the top leaves are likely to suffer on average more disease than the flag leaves. Therefore, disease scored in the top four leaves will better characterize entries in years of low disease development. During favorable years when Septoria can reach the flag leaves, disease scores taken at either the top four or flag leaf level may be used to characterize cultivar response.

Lack of sufficient rains during 1984-85 may have precluded sources

naturally present in the environment to release sufficient inoculum or the movement of the disease up the plant to produce a severe epidemic. The lack of sufficient rains during this season may have prevented pycnidia germination, host penetration, and the movement of the disease up the plant. This is reflected in the small difference found between disease scores of protected and naturally inoculated plots and in the twofold disease severity increase between naturally and artificially inoculated plots. During this season, artificial inoculation was the only procedure by which resistant entries could be differentiated from susceptible ones. In the 1985-86 season, ample inoculum was available in the environment to start the first cycles of the disease through natural infection. Favorable weather conditions contributed to the large disease differences between protected and naturally inoculated plots. Artificial inoculation was not needed during this year to distinguish susceptible from resistant entries.

Changes in ranking in which the entries were classified during the two seasons demonstrates the need for conducting experiments to evaluate disease reaction for more than one year. While during both seasons the most resistant and susceptible entries maintained their ranking some entries varied. Entries 2 and 9 were classified as resistant the first year. Apparently they perform well under low pathogen pressure but are overcome under a higher pathogen challenge. Entries 4 and 8 performed relatively better during the second year. These two entries had much higher disease severity levels during the second year; however, this increase was not as large as it was in most other entries. This situation improved their position in the second

year ranking.

Slightly higher disease severity levels were observed on the protected treatment in the 1984-85 than in the 1985-86 cycle. Disease severity may have been overestimated during the 1984-85 cycle or underestimated during the 1985-86 cycle. Because of the low experience in disease assessment by the researcher it is likely that overestimation may have occurred during the first season. Also, the lack of a high level of disease severity to be used as reference may have slightly biased the disease readings during the first year in which the experiment was conducted.

During the 1985-86 growing season disease severity scores were taken twice, 17 days apart during the grain filling period. Entries such as 1 and 5 showed large increases in disease severity between sampling dates, mainly at the flag leaf level. Entries that did not show an increase were either resistant or susceptible. For the latter situation the plants had most of their leaf area already destroyed at the time of the first scoring. Entries 1 and 5 could have been classified as susceptible at the second sampling date, when their resistance actually held up until late in the season. This result indicates the need to record disease information more than once during the growing season. Since the optimal time for disease assessment may vary from year to year according to the environmental conditions and to genotype differences it may be a safer practice to assess disease severity at least two times during the season. This procedure may allow the identification of "late septoring" cultivars.

Effects on Yield and Components of Yield

The low disease severity levels observed during the 1984-85 season did not affect grain yield. A 5% reduction in the number of seeds per spike was realized when treated plots were compared with the fungicide protected plots. Kernel weight was reduced in some entries while in other entries it remained unaltered. Even though it was not statistically significant, most entries suffered larger reductions in seed number than in kernel weight.

With adequate disease development observed during the 1985-86 season both plot yield as well as the two yield components measured were reduced. The number of seeds per spike and kernel weight were reduced between 5 and 6% respectively. Plot yield was reduced 20%.

Spikes in artificially inoculated plots produced higher seed yield during the 1984-85 than in the 1985-86 season. However, this yield difference at the spike level was not reflected at the plot level. Conversely, it was during the second season that the highest plot grain yields were observed. On protected plots the yield advantage observed in the 1985-86 cycle compared to 1984-85 was of 30%. For nonprotected plots this advantage was only 9% when comparing the two years. Plant density appears to have been partially responsible for the yield differences observed during the 1984-85 cycle between spike and plot yield. The low correlation between spike yield and plot yield during the 1984-85 cycle ($r=0.29$) indicates that spike yield could not be translated directly into plot yield. During this growing season plant density was not uniform and some times suboptimal. Consequently, the low number of fertile tillers in this season may have depressed plot

yield despite the high spike yield. Also the reduced competition among plants may have favored an increase in spike yield. This situation may have also affected *S. tritici* development by providing a more hostile microenvironment than that produced in a denser leaf canopy. The canopy density effect has been indicated as an important factor regulating *S.nodorum* development in short statured wheats (Scott et al., 1982).

The lack of significant yield differences among entries during the 1984-85 season, despite a range of 1.45 ton/ha between entries, can be attributed to the size of the experimental error. The experimental error for the 1984-85 cycle was more than seven times greater than the experimental error during the 1985-86 cycle. During the second season the smaller experimental error allowed for yield differences to be distinguished among entries. Across years and treatments the highest yielding entries were Hill 81, Stephens, and Malcolm, three locally adapted, soft-white wheat cultivars. With the exception of Hill 81 these cultivars had a high septoria tritici blotch severity in both years. However, they are cultivars which possess a high yield potential when grown in the Willamette Valley. Hill 81 was in fact released for this area as it does appear to have more tolerance or resistance to septoria tritici blotch than the others. Since it is taller and later than either Stephens or Malcolm, it may be escaping the disease rather than being resistant.

Effects on Grain Quality

It is generally accepted that one of the important results of

septoria tritici blotch on wheat is the production of shriveled grain (Eyal, 1981). The reduction in test weight observed in inoculated plots during the 1985-86 season confirms this observation.

Grain protein percent and grain hardness, two important grain quality parameters, were not changed by Septoria infection. These results can only be applied to the entries and under the environmental conditions evaluated in this research. They may be used however to formulate guidelines for hard-red wheat production in the Pacific Northwest. At the septoria tritici blotch levels observed in this experiment, modifications to the nitrogen fertilization program for Septoria-diseased wheats seem unnecessary. The same levels of grain protein and grain hardness are likely to be obtained in resistant as in susceptible Septoria-diseased cultivars.

Correlation Between Disease Severity and Yield

In contrast to what was observed under the greenhouse study, no differences were observed in this experiment between correlations involving disease severity of the top four leaves and correlations involving flag leaves. Correlation coefficients obtained during 1985-86 were higher than those obtained during 1984-85. The lack of consistency between correlation coefficients calculated in each season suggests that studies to detect tolerant materials must be conducted over several growing seasons.

During the second season, and based on correlation values, entry 9 was the most tolerant to the disease in maintaining the number of seeds per spike. Entries 1, 4, and 5 tolerated disease mainly by maintaining

kernel weight. These four entries were also the most tolerant to disease when total grain yield is considered.

Comparison Between Greenhouse and Field Results

Only entries 1, 6, 7, and 10 were common to the field and greenhouse experiments. The comparison of correlation coefficients between disease severity and yield or components of yield revealed that entry 1 showed the most consistency between greenhouse and field experiments. Even at high levels of disease severity in both environmental conditions kernel weight was maintained. Similar correlation coefficients between the variables number of seeds per spike and disease severity were observed for the cultivar Stephens in both experiments.

Although only four entries were compared between experiments, it appears that the results obtained under controlled conditions differ from those obtained under field situations. Additional factors beside septoria tritici blotch could affect field results and thus be responsible for this difference. These results point out the need to conduct disease tolerance studies under the conditions in which cultivars will be commercially used as factors other than septoria tritici blotch infection may be influencing grain yield.

Response of entries in the greenhouse and field experiment were more similar for disease severity levels of the top four leaves than for the flag leaves. For the four entries the correlation between top four leaves greenhouse disease scores (six inoculations) and second year field disease scores on artificially inoculated plots was $r=0.77$.

This result is in accordance with previous studies reporting agreement between septoria tritici blotch severity data recorded in the greenhouse and in the field (Brokenshire, 1976).

The four entries studied in both experiments had a higher number of seeds per spike and kernel weight under field than in the greenhouse. This was true for both 1984-85 and 1985-86 field values. This difference could have resulted in the sampling procedure as in the greenhouse all spikes of a given plant were used to calculate the plant average seed number per spike and 1000 kernel weight. In the field, ten spikes were randomly picked from each plot. The number of seeds per spike lost by these four entries was higher in the greenhouse than in the field.

Effect of Planting Dates and Inoculation Procedures on Disease Reaction

In the experiment designed to study the effect of planting dates and *Septoria tritici* inoculation procedures on wheat (Study 3), different levels of disease severity were recorded in each season. The entries used in this study were the same ones used in Study 2. Differences were observed in all treatments with the exception of the late sown (January 20) that was covered with a plastic film after inoculation (treatment 1). The practice of covering plots after inoculations allowed for the development of high levels of disease independently of weather conditions. The largest difference in disease severity between years was observed in the late sown, naturally inoculated plots (treatment 3). The lack of sufficient rains and perhaps of enough naturally occurring inoculum during the first year

may have been in part responsible for the low levels of disease recorded during the 1984-85 cycle. The smallest disease severity difference between years was recorded in the early sown treatments. These plants had a longer vegetative growing period in which to be colonized by *S. tritici*. Perhaps, the favorable conditions for disease development early in the season allowed also for a faster and larger production of secondary inoculum than in the later sown materials.

The highest correlation coefficient during the first year between late and early sown plots was recorded for the late sown, plastic covered treatment. This result suggests that during dry years the practice of covering plots with a plastic film after inoculation would provide the most meaningful information to classify late sown materials. On higher rainfall years, plastic covering may not be advantage. In the high rainfall year resistance of late sown materials was not overridden by artificial inoculation. Breeders may be interested in evaluating disease reaction in segregating late sown materials. These materials may have been late sown after growing for a generation in a greenhouse.

Effects on the Number of Seeds per Spike

The two yield components measured also reflected the different environmental conditions between years. The number of seeds per spike was lower during 1984-85 than during 1985-86 in all treatments with the exception of the one sown on the recommended date for the region (October 25, treatment 5). This optimal planting date in a dry year may have helped to produce a higher number of seeds per spike. Due to

the high levels of disease suffered by the early sown plots (September 25, treatment 4) during the first season the number of seeds per spike were reduced. The high level of disease observed in late sown, plastic covered plots in the 1984-85 cycle did not reduce the number of seeds per spike beyond the number observed in the other late sown treatments. Apparently, the shorter period of time available for these plants to complete their cycle depressed the number of seeds per spike which was not further reduced by Septoria. This same situation was found during the 1985-86 season.

Effects on Kernel Weight

In the 1984-85 season the practice of covering plots with a plastic film layer after inoculation reduced the weight of kernels to levels lower than those found in any other treatment. Under the conditions of the 1984-85 season, the high disease severity levels observed in September 25 and October 25 sown plots reduced the weight of kernels to levels similar to those found on late sown, no plastic covered plots (treatments 2 and 3). In the 1985-86 season smaller differences were found for kernel weight among treatments. Early and October 25 sown plots still had an advantage in kernel weight over the late sown treatments even though they supported, on average, higher disease severity. The longer growing cycle and the more favorable conditions for seed production during this season may have prevailed over the stress imposed by the high levels of disease.

Effects on Grain Quality

Grain protein percent and grain hardness were not modified by the treatments. This suggests that two grain quality parameters somehow remain constant even when sown four months apart. This was true even when different levels of septoria tritici blotch severity were present. However, all entries did not respond in the same way as noted by the high entry by treatment interaction for these variables.

Septoria Tritici Blotch Progress

Following the suggestions made by Vanderplank (1968) disease progress was studied through the use of equations relating disease severity to time. The slope of linear or linearized regression models provided a way of studying the rate of epidemics progress. Four different models were tried in the search of the best and most convenient way to describe disease progress.

After analyzing and comparing advantages and disadvantages of the models studied it was decided to use the linear regression model to analyze disease progress. The regression coefficients of the simple linear regressions obtained using untransformed data were used as observations in the ANOVAs of this experiment. These regression coefficients were obtained for each of the 150 plots of the experiment. Data for the variables, disease severity in flag and top four leaves and disease progress coefficient collected during six sampling dates, were analyzed through this procedure.

Top Four Leaves Disease Progress

The high rate of disease development observed for the top four leaves during the 1985-86 season was due to the more favorable weather conditions. Plants in plots covered with a plastic film after inoculation had approximately the same rate of disease increase in both growing seasons. The favorable conditions for infection provided by the plastic enclosure allowed for good disease development regardless of weather conditions.

Small differences were observed in the rate of disease progress between seasons for the early and October 25 sown treatments. However, the final level of disease recorded in these treatments was higher during 1985-86.

The largest difference between years was noted in the late sown, naturally inoculated plots (treatment 3). This large increase in disease progress rate during the 1985-86 season was probably an effect of the rainfall increase recorded during this season. It may also reflect the availability of sufficient natural inoculum in the environment during that year.

Plastic covered plots had a higher rate of disease progress than plots subjected to the other treatments. For both growing seasons, late sown, naturally inoculated plots had the lowest rate of disease progress. These results suggest the need to adopt special inoculation procedures in late sown plots in order to have a stable disease rate progress from year to year. The covering of plots after inoculation with plastic films would be a satisfactory way to induce disease development.

The rates of disease progress observed in the different entries were in accordance with the disease scores recorded at the last sampling date. The correlation between the rate of disease progress and disease severity recorded at the last sampling date were $r=0.99^{**}$ and $r=0.89^{**}$ (N=10) for the 1984-85 and 1985-86 cycle, respectively. Thus the levels of disease severity recorded at the top four leaves can provide an adequate indication of how disease progressed during the season. Perhaps, this score alone could be enough to describe the rate of disease progress. However, the study of the rate of disease progress may offer the possibility of detecting "late septoring" cultivars. For example, entry 1 which had high levels of disease severity at the last sampling date could only be identified as "late septoring" by its low disease progress rate. High rate of disease progress is confined in these cultivars to the last two or three weeks before senescence.

Flag Leaf Disease Progress

Disease progression results similar to those found in the top four leaves were observed for disease severity involving the flag leaf. Differences in disease progress rate between years were much more dramatic for the flag evaluation than for the top four leaves. When comparing years, the naturally inoculated plots (treatment 3) had a disease progress rate more than ten times greater in 1985-86 than in 1984-85. This result indicates that disease progress rate differences between a conducive and a nonconducive environment are much more marked in the flag leaves. This seems to be a consequence of the way in which

septoria tritici blotch progresses through the plant. In a dry year it may reach some of the top leaves but it may not reach the flag leaf.

Vertical Progress of Disease

The vertical progress of septoria tritici blotch through the plant was measured by the regression of disease progress index versus time. The disease progress index indicates the height reached by Septoria in the plants relative to plant height. The nearer the index value is to one the higher is septoria tritici blotch in the plant. The slope of the regression of disease progress index versus time is the disease progress index rate (DPIR).

Little change in DPIR was observed between growing seasons even though less disease developed during the 1984-85 season. However, not all treatments responded in a similar manner. Late sown, naturally inoculated plots had nearly a twofold DPIR increase between years. This was the consequence of the higher rainfall recorded during the 1985-86 cycle. Also larger amount of naturally occurring inoculum may have been available in the environment during the 1985-86 season. The higher DPIR found in late sown material indicates that the average daily movement of Septoria in the plant was higher in late sown plants. This may have been the consequence of Septoria already having moved up the plant in the early sown material at the time disease height was first recorded. In late sown plants, the movement through the plant was initiated and completed during the period this information was recorded.

The correlation between DPIR and final plant height was r=0.06 and

r=-0.42 (N=10) for the 1984-85 and 1985-86 cycle, respectively. Therefore, under the environmental conditions of the first cycle Septoria is likely to progress through the plant at the same rate regardless of the height of the plant. However, in wetter years, there is some indication that the disease could reach the top of the plant faster in a shorter stature entry. This results agrees with reports by Eyal et al. (1974) who indicated a faster progress of the disease in relation to plant height in a dwarf than in a semi-dwarf cultivar. This was true even when these two cultivars had the same Septoria susceptibility.

The use of the regression of disease height on plant height to study the vertical progress of septoria tritici blotch in relation to plant development as proposed by Eyal et al. (1974) provided similar results to those found for DPIR analysis. However, the slope of the regression line was steeper for the wetter season indicating higher rate of disease development. This regression method did not provide any indication as to whether disease progressed faster in the short or in tall entries.

Effect of Septoria in Selected Morphologic and Physiologic Characters of Wheat in 1985-1986

Study 4 offered the opportunity of analyzing in some detail how selected morphologic and physiologic characteristics of six winter wheat entries were affected by septoria tritici blotch. Entries 1, 3, 4, 5, 7, and 10 were used in this experiment.

Effects on Stem Length

Stem length measurements indicate that plants in plots sprayed with fungicide were shorter than in nonsprayed plots. The repeated application of the fungicide Propiconazole reduced plant height by means of an unknown mechanism. This effect has been previously reported by Camacho-Casas (1986) on winter wheat cultivars.

Effects on Stem Dry Weight

Stem dry weight was reduced by Septoria in the susceptible cultivars Malcolm, Stephens (entries 3 and 7), and in entries 1 and 5. Stem weight of the resistant entry 4 was not affected by the disease. A possible explanation of this finding is that in the highly diseased plants the mobilization of stems stored products, such as carbohydrates, to developing grains may have been higher than in nondiseased plants. This higher mobilization may have come as a compensation for the lower production of assimilates by diseased plants. Alternatively, this difference may have been just the result of less dry matter production by diseased plants. The lack of stem weight reduction in the resistant entry 4 appears to support the theory that less assimilates may have been produced and more remobilized in diseased entries. Also, it is possible that the fungicide application could have increased stem dry weight.

Effects on Stem Dry Weight by Unit of Stem Length

To compare stem dry weight of entries and treatments excluding the effect of plant height, stem dry weight by unit of stem length was

calculated and analyzed. Stem dry weight by unit of stem length was higher in fungicide protected plots. The largest differences between protected and nonprotected plots were found in the susceptible entries 3 and 7.

Effects on Spike Dry Weight

Spike dry weight was higher in protected plots. The largest differences between protected and nonprotected plots were observed in the susceptible entries 3 and 7. Diseased plants produced lighter spikes than healthy ones. These results agree with yield differences found at the plot level. Spikes in diseased plants were lighter due to the 5% loss of seeds and 7% loss of kernel weight.

Effects on Top Four Leaves Dry Weight

The top four leaves of plants on diseased plots were partially or totally destroyed by Septoria. However, dry weight differences between protected and diseased four top leaves were not observed during the last part of the grain filling period. Although not significant, some weight advantage could be observed in protected, susceptible entries compared with nonprotected ones.

Effect on Flag Leaf Disease Progress

Septoria disease progress in flag leaves was monitored with the help of a leaf area meter on excised leaves in 1985-86. In this way, diseased and healthy leaf portions could be separated and their area calculated. The flag leaf disease progress coefficient (FLDPC), which

was the result of dividing flag leaf diseased area by total flag leaf area, indicated how much of the leaf area was being destroyed at each sampling date. Septoria tritici blotch first reached the flag leaves in the unprotected plots of Malcolm and Stephens. These entries lost most of their green tissue by the last sampling date. For the other entries, the disease did not progress in flag leaves at the same rate. For example, entry 1 could have been classified as susceptible if disease scores had been taken only on the last sampling date. This entry was classified as highly resistant at the third sampling date. For "late septoring" genotypes the large rates of disease increase appears to be confined to the last period during maturation. As was previously suggested, the detection of these genotypes may be only possible by recording disease severity scores prior to the major foliage deterioration.

The correlation between stem dry weight by unit of stem length and FLDPC indicates that the reduction in dry weight seems to be associated with the presence of Septoria on the flag leaves. This negative association could indicate that less assimilates were produced in diseased plants.

Weaker correlations were established between FLDPC and plot grain yield or the plot grain yield components. Other factors such as plant density may have also had an effect on plot grain yield and the components.

Comparison of Two Disease Assessment Methodologies

The accuracy of the visual assessment of flag leaf area affected

by septoria tritici blotch was evaluated by comparing it with estimates obtained with a leaf area meter for disease leaf areas affected. On moderately diseased plants actual disease severity values were overestimated by 10.65% by visual means. For highly diseased plants, actual disease severity was slightly underestimated.

The high correlation between these two methods of disease severity estimation indicates that visual estimation of flag leaf area affected by septoria tritici blotch was accurate.

Monosaccharide and Disaccharide Content of Dry Stems

Analysis of the mono and disaccharide content of dry stems provided a partial view as to how the stored soluble sugars were affected by Septoria. Soluble carbohydrates accumulated in stems and sheaths of protected and inoculated plants up to approximately two to four weeks after anthesis with little remaining at maturity. A similar situation for wheat stem soluble sugars has also been observed by other researchers working with wheat (Ford et al., 1979, Austin, 1980).

There are no reports in the literature with reference to the effects of *Septoria tritici* on stem soluble carbohydrate economy. However, observations from other pathosystems may help to understand these effects.

An increase in respiration in diseased compared with healthy plants could indicate that larger amounts of assimilate are being consumed either by the diseased plant or by the fungi. Scharen and Taylor (1968) could not find differences between respiration rate of healthy and *Septoria nodorum*-infected plant organs. This result is

expected to occur in necrotrophic pathogens such as Septoria. Increases in respiration of diseased plants have been reported for biotrophic pathogens (Allen, 1942, Kosuge and Kimpel, 1981).

Relocation to the developing grains of assimilates stored in the vegetative organs has been reported to be of greater importance under stress conditions (Austin et al., 1977, Jenner, 1986). Consequently, it might have been possible that under the stress situation imposed by Septoria in this study, larger amounts of assimilates were mobilized to the developing grains.

Septoria nodorum was found to depress photosynthesis in diseased plants (Scharen and Krupinsky, 1969, Krupinsky et al., 1973). Although photosynthetic rate was not measured in this experiment, it is likely that the same situation may have occurred due to the destruction of photosynthetic active tissues. A direct effect of reduced photosynthesis may be a decline in the production and storage of soluble sugars.

It would appear that any or all of these three processes, increased respiration, increased dry matter relocation, or decreased assimilate production, may have been affected by septoria tritici blotch. Thus, they may have caused the reduction on stem stored soluble carbohydrates and on stem dry weight found in this experiment.

Variation among entries was observed in the amount of stored soluble carbohydrates lost in diseased plants. The susceptible cultivars Malcolm and Stephens showed the largest disaccharide reduction while the resistant entry 4 had the smallest reduction. These two cultivars suffered also the largest monosaccharide losses.

The reduction observed in stored monosaccharides in the unprotected treatments of entry 4 was a contradiction. The average 12% monosaccharide reduction observed in these treatments does not agree with the disease severity levels suffered by this entry. However, artificially inoculated plots of entry 4 were found in Study 2 to have a 17% yield loss.

Monosaccharide and Disaccharide Content of Flag Leaf and Stem Phloem Exudate

The amount of monosaccharides and disaccharides collected from flag leaf phloem exudate was not affected by septoria tritici blotch. This result indicates that healthy as well as diseased leaves exported equal amounts of these saccharides. This was an unexpected result since the flag leaves of some of the entries were heavily affected by the disease at the time exudate was collected. It is possible that differences could not be detected due to the lack of sensitivity of the method used to extract and analyze the phloem exudate. Large error mean square variability was observed among sampling dates for this variable. This indicates large variability of the plant material in the field and/or variability caused by the extracting and analyzing procedures. It is likely that a larger number of leaves would have to be analyzed to detect significant differences if they existed.

Similar problems may have affected the quantification of stem soluble sugar phloem exudate. However, for this variable, higher levels of sugars were collected in exudate of healthy plants during three sampling dates. The different levels of soluble sugars found on the protected treatment were mainly due to the sugar reduction observed

in nonprotected plots of Malcolm and Stephens. This seems to contradict the theory that more assimilates were exported from stems of plants under stress. However, it supports the idea that less assimilates are produced in photosynthesis impaired plants, and therefore, less assimilates could be stored and later remobilized.

Correlations of Stem and Leaf Monosaccharides and Disaccharides

High negative correlations were found between the amount of soluble monosaccharides and disaccharides extracted either from dry stem or stem phloem exudate and the percent of flag leaf area affected by Septoria. This indicates that the economy of these sugars was directly affected by the capacity of the photosynthetic apparatus of the entries. The weak correlation found for soluble sugars exuded from flag leaf phloem may have been the results of the difficulties in quantifying these sugars, a subject which was previously discussed.

Stem weight by unit of length was directly associated with dry stem monosaccharide and disaccharide content. Thus, much of the stem weight change may have resulted from changes in the content of these sugars in the stems. The negative correlation between soluble sugars collected from flag leaf exudate and spike dry weight seems difficult to explain.

Correlations between plot yield and number of seeds per spike with dry stem soluble sugars and stem phloem soluble sugars indicates that these sugars were, at least partially, influencing grain yield. Therefore, any reduction in content of these sugars in the stems is likely to be reflected in grain yield.

The correlations between FLDPC and dry stem total soluble sugar content for individual entries with the exception of entry 4, suggested a decrease of these sugars stored in stems as the severity of Septoria in the flag leaf increased. Entry 3 had lower correlation between FLDPC and dry stem total soluble sugar content than the entry 7, even though these entries suffered similarly levels of disease severity. Some entries may have the capability of partially overcoming the effect of the disease, perhaps, by storing higher amount of soluble sugars in the stems. This could have occurred as a result of increased assimilate production early during plant development. It may also indicate that some entries may not have the capability to remobilize stored reserves at the same rate as other susceptible entries did.

Soluble sugar levels found in dry stem and phloem exudate of wheat plants were related to the presence of septoria tritici blotch in the leaves. These sugar levels can help to explain the physiology of the disease. However, their measurement involves highly laborious procedures which limit their use by breeders in routine screening tests. Geneticists searching for factors regulating the response of plants to invading pathogens may be interested in this approach.

Information obtained from the studies conducted through this research could be useful to plant breeders working with the septoria tritici blotch-wheat pathosystem. Knowledge on field and greenhouse inoculation procedures and disease assessment gained could aid in the design of more efficient screening methodologies. In greenhouse screening two inoculations may be needed to have a clear distinction between resistant and susceptible entries if disease is assessed at the

top four leaves. In field screening artificial inoculation may be needed in unfavorable years for disease development. Late sown material may need to be covered with a plastic film to have good disease development in years in which septoria shows a poor development. The extent of yield and components of yield lost by entries may assist breeders to search for different forms of resistance. Hopefully this information will also convince administrators of research programs to more efficiently allocate resources aimed at solving different constraints affecting crop production.

SUMMARY AND CONCLUSIONS

The object of this research was to evaluate how changes in selected abiotic and biotic factors could affect the wheat-septoria tritici blotch pathosystem. The studies were design to provide the plant breeder with a better understanding of this pathosystem and to develop strategies for identifying resistance to septoria tritici blotch of wheat.

Selected wheat entries with different reaction patterns were evaluated for response to Septoria in greenhouse and field experiments. Effects of the disease on selected morphologic and physiologic characteristics of wheat were also investigated.

The following conclusions were reached based on the results of this research.

1. The inoculation chamber specially developed for this study provided an adequate environment for plant growth and septoria tritici blotch development. The chamber allowed for the control of the humidity at the time of inoculations and thus it permitted a successful infection.
2. More than two inoculations were needed in the greenhouse to maximize disease severity differences among entries. Six inoculations seemed to be excessive with even resistant reaction patterns being overcome. Two inoculations permitted the separation between resistant and susceptible entries by estimating the infected area of the top four leaves. Three inoculations were needed to make such a distinction for the flag leaf.
3. Under the controlled environmental conditions of the greenhouse, the number of kernels per spike was more affected than was kernel

weight by Septoria infection. Production of late tillers was also severely impaired by septoria tritici blotch infection.

4. Disease severity scores assessed at the top four leaves provided better separation between susceptible and resistant entries than did disease severity assessed at the flag leaf when the material was grown in the field during a dry growing cycle. During the high rainfall year both leaf levels were adequate to assess septoria tritici blotch severity.
5. In the dry season Septoria inoculation by means of inoculum naturally present in the environment was not sufficient to distinguish between resistant and susceptible entries. For the wetter season inoculum naturally present in the environment produced disease severity levels adequate for differentiation of entries disease reaction classes.
6. The best way to distinguish between late sown (January 20) resistant and susceptible entries in the dry years was by covering plots after evening inoculations with a clear plastic film during the night. In the higher rainfall year this procedure was not needed to obtain susceptible levels of infection.
7. Disease severity scored at more than one occasion during the growing season allowed for the identification of "late septoring" entries. These entries were also distinguished by analyzing the rate of disease progress in either the top four or flag leaves.
8. Visual assessment of flag leaf area affected by septoria tritici blotch was, in general, an accurate predictor of actual disease severity levels. In plants having from medium to low disease

severity levels actual leaf area affected by Septoria was overestimated by 17%. In highly diseased plants actual diseased flag leaf area was slightly underestimated.

9. In the experiment designed to measure the effects of natural and artificial inoculations, the number of seeds per spike was reduced in artificially inoculated plots. This was true regardless of the growing season. Kernel weight was reduced in these same plots but only in the wetter season. Plot grain yield was reduced in artificially inoculated plots in the high rainfall season. Test weight was also reduced by septoria tritici blotch during this season. No yield reduction was detected in the dry season.
10. During the wetter season kernel weight was reduced in late sown plots (January 20) compared with plots sown on the optimal planting date for the region (October 25). In both seasons the number of seeds per spike was reduced in late sown plots.
11. Grain protein percent and grain hardness were not affected by septoria tritici blotch.
12. Among the different correlations calculated with greenhouse data between yield and disease severity, the highest (absolute) coefficients were observed for total grain yield per plant and disease severity at the top four leaves. The cultivar Yamhill had the lowest of these correlations which indicates a possible level of tolerance to the disease.
13. Correlation coefficients between yield and disease severity calculated with field information during two seasons were inconsistent. Thus, the search for genotypes tolerant to septoria

tritici blotch may need to be carried in more than one growing season. Also, the comparison of these correlations computed for four entries in the greenhouse and in the field were inconsistent. Therefore, the search for tolerant material may need to be carried under the same conditions in which the plant material will be used.

14. Agreement was found between greenhouse and disease severity scores assessed in flag and top four leaves of the four entries common to both experiments. For these entries larger number of seeds per spike and kernel weight was found in the field than in the greenhouse.

15. The regression coefficient of the simple linear regression of disease severity versus time was suitable to study the rate of septoria tritici blotch epidemic progress.

16. Stem dry weight was reduced by septoria tritici blotch in the susceptible cultivars Malcolm and Stephens. Stem dry weight by unit of stem length and spike dry weight were reduced in naturally and artificially inoculated plots. Dry weight of the top four leaves was not affected by the disease during the two dates measured.

17. During the wetter year dry stem monosaccharide and disaccharide content were reduced in naturally and artificially inoculated plants. The amount of monosaccharides and disaccharides collected from flag leaf phloem exudate was not affected by the disease. The level of these sugars collected in stem phloem exudate was smaller in diseased plants during three sampling dates.

Monosaccharides and disaccharides in dry stem and stem phloem exudate were negatively associated with the percent of flag leaf area affected by the disease, but positively associated with stem dry weight by unit of stem length.

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APPENDIX

Appendix Table 1. Pedigree and description of wheat entries included in the study.

Entry 1: (Comet/Gigant//Adam). Soft red line from the Oregon State University Winter x Spring program. Moderate resistant to septoria tritici blotch.

Entry 2: (Nord Desprez/Pullman Selection 101//Blue Bird/Gallo). Hard white line from the Oregon State University Winter x Spring program. Susceptible to septoria tritici blotch.

Entry 3: Cultivar Malcolm (Stephens//63-189-66-7/Bezostaja). Soft white winter cultivar released by Oregon State University. Medium to high tillering. Susceptible to septoria tritici blotch.

Entry 4: (Aurora/Era). Hard red line from the Oregon State University Winter x Spring program. Resistant to septoria tritici blotch.

Entry 5: (Probstorfer Extrem/Tobary 66 = ORCR 8313). Hard red winter line from the Oregon State University Winter x Spring program. Moderately resistant to septoria tritici blotch.

Entry 6: (D6301/Heines VII//Era/3/Buc). Soft white line from the Oregon State University Winter x Spring program. Resistant to septoria tritici blotch.

Entry 7: Cultivar Stephens (Nord Desprez/Pullman 101). Soft white winter cultivar released by Oregon State University. Medium to high tillering, moderated head fertility, and a high seed weight. Susceptible to septoria tritici blotch.

Entry 8: Cultivar Hill 81 (Redmond/Heines VII/Nord Deprez/2* Pullman Selection 101). Soft white winter cultivar released by Oregon State University. Medium to high tillering, moderated head fertility, and a high seed weight. Moderately resistant to septoria tritici blotch.

Entry 9: (Cno/Chr//On/5/53-388/3/An64/Pi//LR64/4/II18427/6/B = ORCR 8512). Hard red winter line from the Oregon State University Winter x Spring program. Moderately resistant to septoria tritici blotch.

Entry 10: (Pumafen//Ciano"s"/Gallo = ORCR 8414). Hard red winter line from Oregon State University Winter x Spring program. Moderately resistant to septoria tritici blotch.

Appendix Table 1. (continued)

Entry 11: Cultivar Yamhill (Heines VII/Redmond(Alba)). Soft white winter cultivar released by Oregon State University. Low tillering, late maturing, medium height, high yielding, and awnless. Large fertile spikes and medium to large kernel. Moderately resistant to septoria tritici blotch.

Entry 12: DYBR 83-84. Introduction from the Diyarbakir Station, Turkey. Early maturing. Highly susceptible to septoria tritici blotch.

Entry 13: Bezostaja 1. Developed in the Kuban region of the USSR. An awnless, hard red, low tillering, large kernel, and winter wheat cultivar. Susceptible to septoria tritici blotch.

Appendix Table 2. Phenologic stage at the time of inoculations of entries grown in a greenhouse to study the effects of *Septoria tritici* inoculations (Study 1). (Phenologic stages according to the Feekes scale (Large, 1950).

Inoculation number	Days from January 1	Entry						
		1	6	7	10	11	12	13
1	-10	7/8	5/6	5/6	5/6	5/6	7/8	7/8
2	5	8/9	7/8	7/8	6/7	7/8	10/10.1	8/9
3	19	9	8/9	8/9	8/9	8/9	10.5	9
4	32	10.5	9	9/10	9	9/10	11	10.5
5	41	10.5	10	10	10	10.1	11	10.5
6	51	11	10.1	10.1	10.1	10	11	11

Appendix Table 3. Key of treatments utilized to study the effects of *Septoria tritici* inoculations and planting dates in 1984-85 and 1985-86 (Study 3).

Number	Treatment
1	Late sown (Jan. 20), plastic film cover after inoculation
2	Late sown (Jan. 20), artifitial inoculation
3	Late sown (Jan. 20), natural inoculation
4	Early sown (Sept. 25), artifitial inoculation
5	Recommended sowing date (Oct. 25), artifitial inoculation

Appendix Table 4. Schedule at which entries utilized to study the effects of *Septoria tritici* on selected morphologic and physiologic characters of wheat in 1985-86 were sampled (Study 4).

Sampling Number	Entry					
	1	3	4	5	7	10
1	139	143	143	139	141	141
2	146	150	150	146	148	148
3	153	157	157	153	155	155
4	160	164	164	160	162	162
5	167	171	171	167	169	169
6	174	178	178	174	176	176
7	188	192	192	188	190	190

Appendix Table 5. Growth stage at which entries utilized to study the effect of *Septoria tritici* on selected morphologic and physiologic characters of wheat in 1985-86 were sampled (Study 4). (Growth stages according to the Feekes scale (Large, 1950).

Sampling Number	Entry					
	1	3	4	5	7	10
1	10.5	10.2	10.1	10.2	10.2	10.2
2	10.5.2	10.5.1	10.2	10.5.1	10.5.1	10.5.1
3	10.5.4	10.5.4	10.5.2	10.5.4	10.5.4	10.5.4
4	11.1	11.1	10.5.4	11.1	11.1	11.1
5	11.2	11.2	11.1	11.2	11.2	11.2
6	11.3	11.3	11.2	11.3	11.3	11.3
7	11.4	11.4	11.3	11.4	11.4	11.4

Appendix Table 6. Heading dates of entries grown in a greenhouse to study the effects of *Septoria tritici* inoculations (Study 1). (Days from January 1).

Entry	Days to Heading
1	37.84 e
6	66.95 a
7	62.91 c
10	65.37 b
11	60.00 d
12	21.41 g
13	34.93 f

Means followed by the same letter are no significantly different at the 0.01 probability level (Fisher's Protected LSD).

Appendix Table 7. Summary for meterological data for Corvallis, Oregon (1984-85).

	Average 1/ temperature, °C			Radiation Langley	Evaporation mm	Precipitation cm
	Max.	Min.	Mean			
September	23.7	8.6	16.2	362	117.90	1.88
October	15.0	5.4	10.2	183	36.10	11.81
November	10.7	3.9	7.3	97	------	34.42
December	6.6	-0.1	3.2	75	------	10.18
January	5.8	-2.2	1.8	101	------	0.63
February	9.2	-0.1	4.5	169	------	92.70
March	11.7	1.1	6.4	290	------	12.55
April	16.8	5.5	11.1	392	81.00	26.70
May	19.6	6.0	12.8	498	130.60	23.90
June	24.1	8.6	16.3	616	172.00	56.40
July	30.6	11.3	21.0	640	248.70	13.70
August	27.4	9.6	18.5	547	190.80	Trace

1/ Observations were taken from Hyslop Field Laboratory.

Appendix Table 8. Summary for meterological data for Corvallis, Oregon (1985-86).

	Average 1/ temperature, ^{0}C			Radiation Langley	Evaporation mm	Precipitation cm
	Max.	Min.	Mean			
September	22.0	7.6	14.8	342	107.25	1.98
October	17.6	4.7	11.1	225	74.25	9.88
November	7.1	-0.2	3.4	111	------	11.91
December	4.5	-3.6	0.4	11	------	9.45
January	9.7	2.1	5.9	89	------	16.59
February	10.0	3.0	6.5	133	------	25.15
March	15.6	5.3	10.4	290	------	7.72
April	15.1	4.1	9.6	381	73.50	4.67
May	18.7	6.9	12.8	496	94.00	6.35
June	25.2	10.6	17.9	578	155.50	0.79
July	24.6	10.0	17.3	547	166.00	2.92
August	30.6	11.3	20.9	516	203.20	0.00

1/ Observations were taken from Hyslop Field Laboratory.