Effect of common root rot on yield components of spring barleys
by William Edward Grey

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Plant Pathology
Montana State University

Abstract:
Common root rot of spring barley caused mainly by Cochliobolus sativus (Ito and Kurib.) Dreschal ex Dastur has been responsible for considerable losses in grain yield in the North American prairies. Four methods of inoculating barley plants with Cochliobolus sativus were evaluated for their effectiveness in imposing uniform disease pressure.

In 1979 at Bozeman, Montana, C. sativus infested oats sown in the same furrow as seed of the test cultivar did reduce plant emergence and yield. In 1980, this method was compared with the use of natural soil inoculum. Use of C. sativus infested oats did not substantially improve the differentiation of cultivars with intermediate disease ratings over the use of naturally infested soil at a site with a history of CRR.

The effects of Common Root Rot on components of grain yield in sixteen barley cultivars which were agronomically adapted to Montana and representative of the four barley types: Hannchen, Smyrna, Coast and Manchuria, were studied at Bozeman, Montana in 1980. In spite of the mean increase in disease ratings in C. sativus inoculated plots, the high soil moisture levels and moderate temperatures during maturation negated the early pathogenic effects of C. sativus, resulting in no net change in yield. Hannchen and Smyrna type cultivars had a significant reduction in fertile tillers due to C. sativus which was compensated by increased kernels per head and kernel weight. Coast and Manchuria type cultivars responded to a slight decrease in fertile tillers by increasing the number of kernels per head. A combination of increased number of kernels and increased disease rating due to Common Root Rot resulted in decreased kernel weight in Coast and Manchuria type cultivars.

A barley plant is subjectively placed in one of four disease classes based upon the extent of discoloration on the subcrown internode due to Common Root Rot. In a population of plants, the number of plants per each disease class is used to calculate a weighted average, or disease rating. Computations performed by a step-wise discriminating function on the percentage of plants in each of four disease classes, indicated that the severe class was the most discriminating class among cultivars, followed in importance by the healthy class.

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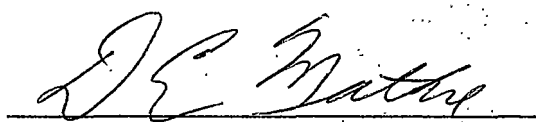
Approved:



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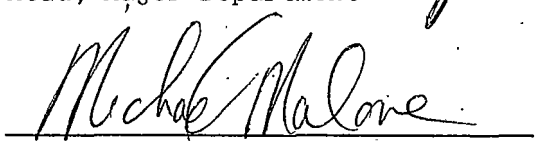

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ABSTRACT

Common root rot of spring barley caused mainly by Cochliobolus sativus (Ito and Kurib.) Dreschal ex Dastur has been responsible for considerable losses in grain yield in the North American prairies. Four methods of inoculating barley plants with Cochliobolus sativus were evaluated for their effectiveness in imposing uniform disease pressure. In 1979 at Bozeman, Montana, C. sativus infested oats sown in the same furrow as seed of the test cultivar did reduce plant emergence and yield. In 1980, this method was compared with the use of natural soil inoculum. Use of C. sativus infested oats did not substantially improve the differentiation of cultivars with intermediate disease ratings over the use of naturally infested soil at a site with a history of CRR.

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INTRODUCTION

The term "Common Root Rot" (CRR) has been widely used to designate a group of diseases that are characterized by necrosis of the roots, crowns, and stem bases of wheat and barley. CRR generally occurs on individual plants growing in competition with healthy ones. The most important fungus of the CRR-complex is Cochliobolus sativus (Ito and Kurib.) Drechsler ex Dastur. Loss surveys in the prairie provinces of Canada have produced estimates of an average loss in wheat for the years' 1969 to 1971 of 5.7%, and in barley for the years' 1970 to 1972 of 10.3%. The incidence and severity of lesioning on subcrown internodes in a population of plants have been used as the index of disease intensity and the resistance of cultivars. The disease index based on the mature plant grown in the field has proved to be consistent over several locations and years, whereas, the seedling reaction test has not been indicative of adult plant reaction. The primary effect of severe CRR infection on the grain yield of spring wheat has been to reduce the number of fertile tillers per plant and the kernels per head.

The purpose of this study was to develop techniques to measure the response of barley to CRR utilizing 16 cultivars with good agronomic adaptation to Montana and representative of the four types of barley: Hannchen, Smyrna, Manchuria, and Coast. Three objectives were considered:

1) To determine the effectiveness of a screening program to improve the resistance of barley and to develop the methods to

insure uniform inoculation pressure by C. sativus.

2) To determine which is the most predictive or discriminating class of the standardized four disease categories in predicting a cultivar's resistance to CRR.

3) To determine the response of barley to CRR as measured by the plant's yield components.

The refinement of techniques in evaluating the barley plant responses to CRR by both disease reaction and yield components may increase the efficiency by which plant breeders may improve the grain yield of barley.

LITERATURE REVIEW

Common Root Rot (CRR) is a prevalent disease of wheat and barley in the prairie provinces of Canada (33,42), the Great Plains of the United States (3), New South Wales and Southern Queensland of Australia (5), and Brazil (17). Several fungi have been implicated as the cause of the discoloration and rotting of lower leaf sheaths, culms, crowns, subcrown internodes and roots. The most important is Bipolaris sorokiniana (Sacc. in Sorok.) Shoem (=Helminthosporium sativum Pammell, King and Bakke), which is the conidial state of Cochliobolus sativus (Ito and Kurib.) Drechsler ex Dastur (53). To a lesser extent the fusaria are isolated from diseased tissue. Fusarium roseum (Link emend. Snyd. and Hans.) f. sp. cerealis 'Graminearum' (=F. graminearum Schwabe) and F. roseum f. sp. cerealis 'Culmorum' (=F. culmorum W. G. Smith) (2) are associated with foot rot and root rot in the Pacific Northwest (16). The Graminearum population responsible for foot rot belongs in Group I whereas Group II is responsible for head blight and scab. Only Group I is associated with foot rot in the Pacific Northwest and in Queensland, Australia (5). Both F. roseum 'Acuminatum' (=F. acuminatum Ell. and Ev.) and F. culmorum were recovered in lower percentages as compared to C. sativus in the prairies of Canada (23).

Symptoms and Histology

The first symptoms of infection on wheat (Triticum aestivum L. Thell.) and barley (Hordeum vulgare L. emend. Bowden) appear as brown lesions on the lower leaf sheaths near the soil line and/or on the subcrown internode. In the western Canadian prairies infection originates from conidia or from mycelium in infected plant debris in the soil usually at the postseedling stage (9). Lesions appear as spots on the subcrown internode two to three days after infection, later expanding into linear streaks. Resistant cultivars of wheat and barley have more pinpoint lesions whereas susceptible cultivars have more linear lesions (28).

Cell wall degrading enzymes and sharp infection pegs under the appressoria both are involved in the penetration of the plant epidermis (28). A sheath, or lignin tuber, forms beneath the cell wall surrounding each infection peg. Lignin tubers contribute little towards host resistance since they occur in both resistant and susceptible cultivars. The infection pegs eventually grow through the lignin tuber and develop branching hyphae, both intra- and intercellularly. In severe infections the occlusion of phloem and xylem vessels is associated with lignin-like materials that may be decomposed host tissues, but the stele is often left undamaged (28). The debilitating, rather than

acute endemic nature of CRR, may be attributed in part to the cortical decay by C. sativus of subcrown internodes.

Disease Loss Assessment

Assessment of losses to CRR is a complex problem dependent upon such factors as time and intensity of infection, inoculum level, and varietal and environmental interactions. Furthermore, C. sativus is present in most fields and it has not been possible to obtain disease-free control plots for comparison. Machacek (37) was the first to estimate the percent yield loss to CRR on the basis of grain weights of clean plants as compared to CRR plants in mixed stands. Using this technique, extensive surveys have been conducted by the Canadian government with an estimated average loss in wheat for the years' 1969 to 1971 of 5.7% (33) and in barley for the years' 1970 to 1972 of 10.3% (42).

McKinney (39) was the first to separate plants with CRR into categories based upon the degree of discoloration on the subcrown internode. The generalization that the mean grain yield per plant decreases with increasing disease severity has been supported by several researchers (33,42,60). Furthermore, there is a decreased number of heads or tillers per plant in severe as compared to clean categories (29, 60).

A disease rating score has been used that attempts to quantify the relationship between disease severity and the percentage of diseased plants. Numerical values of 1, 2, and 4 for spring wheat, and 2, 5, 10

for barley, are intended to represent the proportional reduction in grain yield in the disease classes slight, moderate, and severe, respectively, relative to the yield of clean plants. Each value is multiplied by the number of plants in its respective disease category. The products of the three disease categories are added together, and the sum divided by the total number of plants times the maximum class value. This disease index does not directly calculate yield loss but is based only on past losses suffered by plants in each category (56).

In wheat, Tinline and Ledingham (56) found a good correlation between high resistance and low yield losses. In barley, on the other hand, some cultivars of intermediate disease reaction showed the least yield reduction (42). Many factors influence grain production and may mask the effect of CRR on yield. This makes a simple correlation between disease rating and yield unlikely (56).

Disease Progression

Early season infection may give rise to poor emergence or stunting of the seedlings. When C. sativus infected seed was planted in the field, the tendency of wheat plants to recover from initial stunting was measured by determining the total leaf area and grain yield (47). Once the seedlings were placed in a favorable environment, recovery in leaf area was complete by the time the fifth leaf appeared in Reward and the seventh leaf in Thatcher. Yield was enhanced by inoculation in

Reward but equal to the controls in Thatcher (47).

Recovery from early stunting due to CRR in barley with adequate moisture and nutrients has also been observed in southern Australia (44). However, Claremont barley seed, heavily infested with C. sativus and planted in Scotland, was responsible for reduced stands that contributed 24.8% and 71.2% of the total yield loss in 1973 and 1974, respectively (62). There was an overall stand reduction of 20%. The remainder of the yield loss was attributed to subsequent losses in heads per plant, seed number per head, and seed weight. Under these growing conditions, infected plants did not have more heads per plant than did healthy plants. However, increases in heads per plant occur when low populations are produced artificially by low seeding rates (62). Therefore, tillering may have been affected by C. sativus.

The exact time of the earliest initial infection is not known. Isolations from subcrown internodes of spring wheat, regardless of symptom expression, four weeks after seeding showed that 50% yielded C. sativus, and at five weeks the figure rose to 85% (59). At six weeks, 100% of the tissues exhibited discoloration and C. sativus was isolated from 100% of the subcrown internodes. Infection can also occur later in the growing season. The rate at which plants become diseased has a bearing on the overall severity of the disease at crop maturity. For example, the infection rates (as measured by the percentage of diseased plants versus time) were as follows for Manitou spring wheat in Canada:

1969, 0.99% plants per day; 1970, 1.32%; and 1971, 1.96%. The infection rate in 1969 was slower than that in both 1970 and 1971 because the onset of disease was later and there was correspondingly less disease at the end of the growing season (59). This may have been due to cooler spring temperatures and higher rainfall in 1969 (46) but no reason was proposed (59).

In controlled growth chamber tests, the vertical lesion spread on subcrown internodes of Manitou wheat was rapid at the beginning, tapering off with time, to give an average of 0.3 - 0.5mm lesion extension per day (58, 59). The disease severity and the percentage of diseased plants progressed at similar rates over the same period of time. Apparently, increases in lesion size did not occur and/or many of the initial lesions that formed during the first 60 days failed to develop. Manitou is a cultivar with fairly good resistance but too little is known about the effects of environmental factors on disease development to speculate on this cultivar's apparent ability to slow the progress of lesion development.

Interactions with the Fusaria

The frequency of isolation of C. sativus from mature plant and seedling tissue is greatest in the presence of high spore populations in the soil (9). However, there is a poor correlation ($r = 0.3 - 0.6$) between the percentage of tissue discolored and the number of subcrown

internodes yielding C. sativus (23). This may be due to the fact that other fungi are also responsible for the discoloration (23,44). Furthermore, the population of C. sativus conidia in the rhizosphere can be quite low with recovery of the fungus from subcrown internodes still possible. In the absence of C. sativus, Fusarium spp. are often recovered from 'clean' subcrown internodes and from plant tissue in soils with low numbers of C. sativus conidia (6). To answer the question of whether multiple infections by C. sativus and F. roseum can occur on subcrown internodes, Tinline (55) studied the interaction of both genera in a greenhouse experiment. There appeared to be no difference in the type of lesions produced by either C. sativus or F. culmorum and F. acuminatum, nor were there differences in disease reaction between cultivars of spring wheat as compared to the reaction normally apparent under field conditions. An antagonism between C. sativus and F. culmorum or F. acuminatum did occur, which depended upon which fungus first colonized the subcrown internode. The fusaria were capable of invading and establishing themselves on C. sativus colonized tissue. However, C. sativus was a poor invader if the fusaria were first in possession of this tissue. Therefore, in determining the causal agent for discoloration in the case of multiple pathogen infections, C. sativus can be assumed to be the primary pathogen (57). However, the role played by Fusarium spp. in discoloration of the subcrown internode can vary with the location. For instance, in Washington F. culmorum is the primary pathogen (16).

Pathogen Survival and Variability

Studies by Chinn et al., (8,9) on spore populations in 100 Canadian fields in 1959 and 47 in 1960, using the floatation-viability method, yielded consistent averages of 150 and 178 conidia per gram of soil on a dry weight basis, respectively. The correlation between seedling disease and the spore population in greenhouse tests was highly significant. This same relationship was not found for mature plants in the field. It has been suggested that in addition to inoculum density, soil type (10), moisture level (46), and other organisms in the soil may influence the severity of disease (1,40).

Evidence of microbial organisms perforating the walls of pigmented conidia has been obtained using electron microscopy. Free living mycophagous amoeba inhabiting arable soils were capable of perforating C. sativus conidia (1). The activity of perforating agents in the soil increased during high soil moisture and decreased with drier soils (40). This may help explain Chinn's earlier observation that conidia of C. sativus survived for longer periods of time in dry soils as opposed to soils at field capacity (9).

If infection is measured as the disease reaction on the mature plant, then the development of disease seems to be independent of the spore number in the soil until a threshold level is reached of approximately 27-46 conidia per gram of soil (6). The most reliable technique for determination of inoculum levels of C. sativus has been the floata-

tation-viability method (9). A selective medium has been used for tissue isolations but it is not useful in quantitative determinations of infective propagules of C. sativus in the soil (51). Infected plant debris will often yield Fusarium spp. that mask the presence of the slower growing C. sativus, even on this selective medium (51).

Genetics of Virulence

Genetic studies involving C. sativus have been hindered by its production of multinucleate, heterokaryotic conidia, and intertwining ascospores (54). Sexual reproduction is controlled by one gene but modified by additional genes (54). Progeny of single haploid ascospores had varying colony morphologies, but all were highly virulent. Virulence was epistatic over avirulence. On spring and durum wheat, virulence was controlled by at least two genes while on barley there were two to four genes (26). Although the sexual stage has not been detected in the field, recombination to produce new strains is possible since parasexual recombination has been observed in somatic hyphae that have double the number of chromosomes and consistent pairing of homologous chromosomes (27). At present there is no indication of distinct biotypes within C. sativus since the cultivars tested exhibit no differential response to infection (11,20).

Effects of Cultural Practices

The effects of stubble management, soil fertility, and water retention as they influence CRR have been examined (34,61). The early practice of moldboard plowing with the complete inversion of the soil often resulted in a reduction of root rot in the seedling stage when compared to that occurring with surface tillage. In the mature crop, however, the differences in root rot frequency were no longer observed (31).

In Manitoba, there was no obvious change in the percent of root rot infection (75% infected roots) after six years of continuous wheat, except that in the first year following a fallow period there was a slight reduction (45% infected roots) (18). Continuous cropping of barley had no effect on root rot (12).

There are conflicting reports on the effects of nitrogen fertilizer on CRR. The use of ammonium fertilizer, when compared to no added fertilizer, slightly increased the severity of root rot (19% vs. 15%) on spring wheat growing on residue-free soil (32). On the other hand, in Saskatchewan, with Manitou wheat, nitrogen applied to stubble reduced the percentage of diseased plants but not the disease severity early in the season, but subsequently no effect was observed (61).

Excess phosphorus generally had little effect on the final yield and severity of root rot in barley (43) and Manitou wheat (61). Phosphate fertilizer did have the tendency to reduce root rot severity at midseason but by harvest, differences were no longer present (61).

Decreasing fertilizer concentration below the optimum for growth predisposed the plant to more severe disease damage while the use of fertilizer in excess of recommended rates did not materially affect the plants' response to the pathogen and is impractical as a means of control for CRR (4,61).

Herbicide (2,4-D ester) had no effect on CRR (61). On a crop grown on summer fallow, supplemental irrigation 71 and 84 days after planting had no appreciable effect on the percent of diseased plants compared to non-irrigated checks (61). However, the disease severity on plants growing on dryland as compared to irrigation can be greater and can have an adverse effect on yield greater than that due to drought alone (46).

Seeding date had little effect on the percent yield loss due to CRR in eastern Canada (29) but in the western provinces a delay of ten days after the average time for planting resulted in reduced infection. But late seeding cannot be safely used on the western prairies because of autumn frost hazard (3).

The seedling blight phase of CRR on the prairies is not considered to be of great importance since there is little evidence of seed borne inoculum. Stand reduction of up to 38% from seeds heavily infested by C. sativus resulted in no yield loss (13).

The depth of seeding may vary during planting and some seed are left near the soil surface. These plants have short internodes and may or may not be invaded by C. sativus and Fusarium spp. Observations

indicate that shallow seeding results in lower root rot severity (33), but there has not been a reliable method developed to assess the effects of CRR on plants with a short or nonexistent subcrown internode.

Crop rotation as a means of controlling CRR in wheat has been studied utilizing disease ratings and tissue isolations (3), and measurements of conidial populations in the soil (6). Disease ratings based on the discoloration of subcrown internode decreased with each successive year of a non-susceptible crop (31,34). However, various crop sequences did not alter the frequency of isolation of C. sativus from tissue of wheat. This is interesting in view of the fact that summer fallow, a crop of oats, sweet clover, or some non-susceptible crop, actually reduced the CRR damage, or severity, on the following crop of spring wheat (3). Oats are highly resistant to C. sativus, but will still maintain a significant number of conidia in the soil (6). Rape is not considered to be a host crop for CRR since the level of conidia per gram of soil decreased from 235 to 46 after a three year rotation. But the decline of conidial populations following the cultivation of rape was not any faster than a decline attributal to aging and various environmental and microbial factors (7). Enough conidia appear to survive, even after five years of a non-host crop, making crop rotation an impractical means of control (3,6).

Inoculation Techniques with C. sativus

Artificial inoculation techniques with C. sativus have been used to overcome the inherent variability in inoculum density of this pathogen in soil and to produce uniform inoculation pressure for screening the resistance of wheat and barley cultivars. Sallans in 1933 reviewed the then current methods used and recommended soaking seed in conidial suspensions for 18 to 27 hours at 24°C prior to planting as a means of insuring uniform infection for field testing of seedling reaction (45). Workers have continued to use this method for seedling reaction tests (21). The addition to soil of a solid medium overgrown with the fungus has been tested utilizing various substrates such as oats and vermiculite or sand amended with cornmeal or potato broth (20,21). Although there appears to be a poor relationship between seedling and adult plant reaction, the seedling test has continued to be used for screening the aggressiveness of isolates (21). Use of naturally infested soil, however, is relied upon for determining mature plant reactions to CRR in most current studies. The seed is deeply sown to a maximum depth of 9 cm to encourage the development of a long subcrown internode (49,52,59).

Resistance in Barley

Researchers at Ottawa, Canada, have utilized a sand-cornmeal inoculum in greenhouse pots to evaluate root rot and seedling blight in barley (35,36). Based upon the general vigor of seedlings grown for 21

days in a controlled growth chamber, the seedlings were subjectively placed in one of five disease categories. Over 770 cultivars and selections of barley were tested. Anoidium, Br3962-4, Lenta, and Opal B showed the highest resistance, while Olli was used as a universal susceptible cultivar for comparison. The reaction of F_3 families from crosses between two resistant cultivars, Anoidium and Br3962-4, with Olli suggested the presence of dominant genes for resistance in Anoidium and Br3962-4. However, the disease development was strongly linked with climatic conditions as the cultivar resistance was not clear cut, suggesting that additional genes may play a role in resistance (25).

Another method of evaluating cultivar response to CRR has been to determine yield reduction. In some cases a cultivar may yield well in spite of being heavily infected. This appears to be the case for Betzes and Galt (41). The discrepancy between a yield test and a seedling reaction test for the evaluation of cultivar resistance can be illustrated with Betzes. In the yield test Betzes had the smallest yield reduction; however, in a greenhouse seedling reaction test it was classified as susceptible (15,20). Screening for disease reaction alone may have overlooked this cultivar's ability to yield well in the presence of C. sativus. CI 8969 showed the reverse reaction in that resistance was observed in seedlings while the mature plants were rated as susceptible in the field (14,15).

Barley seed size strongly influenced the seedling reaction to CRR

(15). Increased kernel weight was proportional to decreased disease index. The large seed of Olli, the susceptible standard, produced seedlings with greater resistance than seedlings from smaller seeds. However, no correlation was found between seed size and adult plant reaction (15). A seedling test in which the mean height of each clump of plants was determined, along with the mean length of the root system, indicated that winter types of barley had a higher level of resistance to CRR than the spring types (11).

Resistance in Spring Wheat

The discrepancy between seedling reaction and adult plant reaction to CRR was also observed in spring wheat. The wheat line 680 from Canada has the highest field resistance but is very susceptible as a seedling (21,22,48). Earlier work with Marquis, Thatcher, and McMurachy showed a seedling mortality of 10, 19, and 79%, respectively (50). The reverse was true for their field ratings based on the percentage of subcrown internode discoloration, i.e., 47, 46, and 32%, respectively (57). Line 680 has McMurachy as one of its parents. While seedling reaction does not seem to always be a reliable indicator of mature plant resistance, disease ratings based on the discoloration of the subcrown internode of mature plants have remained consistent in field tests over several locations (49). The selections 680, 635, and 1639 have had one fourth the number of diseased plants as the relatively resistant

and widely grown Thatcher, indicating that selection for resistance can be accomplished (49).

During the three year period 1969 to 1971, Manitou was the most widely grown cultivar on the Canadian prairies, averaging an annual loss of 5.7% due to CRR. Lines have been developed with better resistance than Manitou but their agronomic qualities are relatively poor. A screening of 5500 lines of T. aestivum from around the world indicated that good sources of resistance are available, but no commercial varieties have yet been released that are highly resistant (24). Progress in developing resistance to CRR in hard red wheat has been made in Canada when their lines are compared with cultivars from North America, Australia, Kenya, and Mexico (24). Line 680, highly resistant in Canada, was also the most resistant in Australia (44). There also appears to be good resistance in the soft white wheats, e.g., Festival (63) and the durum wheats, e.g., Edmore and Wakooma (52).

Depending upon the parental material used, the resistance in spring wheat has been interpreted as being either polygenically or simply inherited. Because of the problem with plant escapes, the selections chosen with high resistance must be screened in subsequent years to insure consistent reaction type. Sallans and Tinline (48), being careful not to select plants that were disease escapes, have been able to develop wheat lines more resistant or more susceptible than either parent. These selected lines were consistent in their reaction for two

years at four locations. The parental lines were Thatcher, Willet, McMurachy, PI 94562-1, and PI 4309. The inheritance of resistance in progeny from these parents was concluded to be polygenic in nature (49).

Utilizing a different combination of parents, workers at Lethbridge found resistance to root rot in Thatcher to be simply inherited. The solid stem line, CT 733, is resistant to wheat stem sawfly (Cephus cinctus Norton), but very susceptible to CRR. This line was crossed to the hollow stem, root rot resistant cultivars, Thatcher and Pembina. The F_3 progeny were screened for resistance to CRR in greenhouse seedling tests. The progeny did not appear to segregate for reaction to CRR. The mean disease rating of the F_3 progenies was 96%, indicating that resistance was recessive. A theoretical model based on one gene did not fit the observed data; therefore they postulated that a major recessive gene working in conjunction with one to two minor genes lowers the disease reaction (38).

Cytological analysis confirmed the existence of a major gene for susceptibility of the line S-615. The minor genes that were postulated by McKenzie and Atkinson (38) appear to be on chromosomes 2B and 2D. The substitution of chromosome 2B and 2D from Apex (root rot resistant and hollow stem) for their homologs in S-615 (root rot susceptible and solid stem) increased the resistance of S-615, but not to the same extent as did the substitution of chromosome 5B (38). Fortunately the genes for hollow stem that are on chromosome 2B and 2D are not linked to the minor

genes for CRR resistance on these same chromosomes. Fortuna is an example of a cultivar with increased resistance to CRR combined with sawfly resistance (30).

Effects of CRR on Yield Components

Except for the work on seed borne inoculum of C. sativus on Claremont barley (62), the only work on the effects of CRR on yield components of wheat and barley for dryland conditions has been with spring wheat on the Canadian prairies (46,60). The progress of disease on Manitou was followed for each of the four disease categories over a three year period as measured by its effects on number of tillers per plant, weight per head, weight of grains per head, number of grains per head, and 1000 kernel weight. There was a good correlation between increased disease severity and decreased values of all five variables. The severe disease class stood out as the one most affected in all variables except 1000 kernel weight. The f value from an analysis of variance for each yield component studied separately, was largest for number of tillers per plant and number of grains per head, suggesting that these two components are the ones most affected by CRR (60).

CHAPTER I

INOCULATION METHODS TO INSURE UNIFORM DISEASE PRESSURE

Procedures for screening cultivars or lines of barley for resistance to CRR are complicated by the variability of naturally occurring inoculum in the soil which results in 'mixed stands' of infected and healthy plants. To avoid this variation in inoculum, four methods of inoculating field grown barley with C. sativus were evaluated for their effectiveness in reducing the number of plant escapes and insuring uniform infection.

Materials and Methods

Inoculation was done with a mixture of two isolates of C. sativus, #214 and 195, taken from discolored subcrown internode tissue of barley from Highwood, Montana. Each isolate was grown separately on 2% potato dextrose agar (HPDA)(Difco) adjusted to pH 5-6, for four to five days at room temperature, ~22°C.

Inoculation Methods

Method #1 -- Infested oat kernels were prepared by adding 90 ml of distilled water to 140 g of oat kernels in a one quart canning jar. The jar mouth was covered by a metal lid with a 2 cm diameter hole, on top of which was placed a #4 Whatman filter-paper, 7 cm diameter, for ventilation of gases and minimization of microbial contamination. The

jar with oats was autoclaved at 121°C for 45 minutes. Plugs of C. sativus mycelium and conidia from both isolates, #214 and 195, were added to the cooled oat kernels and allowed to grow for 14 days. The infested oats were spread to air dry, sieved through a 1 cm square mesh, and individually packaged into 20 g lots. One 20 g packet of oat kernels infested with C. sativus was sown in the same furrow as the test cultivar. The control row was sown with 20 g of non-infested autoclaved oat kernels. Both rows were 3 m long.

Method #2 -- A straw medium was prepared by stripping dried Cheyenne winter wheat culms of the outer leaf material, cutting the stems to 13 cm lengths, and placing 20 g of stem material in a clean one quart canning jar. Lid, filter-paper, and autoclaving procedure were the same as in Inoculation Method #1 above. A heavy conidial suspension in 40 ml of sterile water was added to the bottom of the jar and wicked up by the dry straw. By the end of 14 days at room temperature the stems were completely colonized by sporulating conidia and mycelium of C. sativus. The infested straw was air-dried and chopped into 1 cm pieces for packaging. Two 10 g packets of chopped straw, either infested or autoclaved, were sown in each 3 m row with the test cultivar, inoculated and control, respectively.

Method #3 -- A heavy conidial suspension was harvested by rinsing the surface of PDA cultures of both isolates with sterile water and combining the suspension before soaking the barley seed in it. One

hundred grams of seed of each cultivar was soaked four hours, air dried, and planted the following day. Four replications of each cultivar were taken from the 100 g infested seed lot. All test cultivars were inoculated with a sample from the stock conidial suspension. A fresh conidial suspension was prepared for each planting date. Excessive handling of the infested seed was kept to a minimum but 150 infested seeds per replication of a cultivar were counted and packaged individually. The dried seed, either infested or sterile water control, was sown in the inoculated or non-inoculated rows, respectively.

Method #4 -- Because of the inability of the seeder used in the 1979 experiment to penetrate deeply into the prepared seed bed, soil was mounded over the furrow in an attempt to produce a long subcrown internode on the barley plant. Oat kernels infested with C. sativus were placed on top of the furrow after planting of the test cultivar. Additional soil was then mounded over the furrow to a height of 8 cm to simulate deep planting.

Seed Source and Preparation

Test seed of 'Bonanza', 'Betzes', 'Galt', and 'Centennial' were obtained from Dr. E. A. Hockett, USDA-ARS, Bozeman, Montana. Seed of each cultivar were sieved to pass through a 6.5/64 x 3/4" (0.26 x 1.91 cm) mesh and remain on a 5.5/64 x 3/4" (0.22 x 1.91 cm) mesh. One hundred fifty seeds were counted with an electronic seed counter, packaged, and planted in each 3 m row (rate ∿7 g/3 m row).

Field Plot Design

The plot design was a split-split plot. The first major split was the two planting dates, May 3 and June 5, 1979. Each planting date was randomly split among the four cultivars, Bonanza, Betzes, Galt, and Centennial. Within each cultivar a basic 12 row plot consisted of eight treatment rows enclosed by two border rows on each side. The four inoculation methods as paired rows, i.e., inoculated with C. sativus and its adjacent non-inoculated row, were randomized within a test cultivar. The experimental design was replicated four times and planted at the Montana Agricultural Experiment Station Farm 5 miles west of Bozeman, hereafter referred to as Bozeman, Montana.

Data Collection

Emergence data were collected at the two leaf stage of growth. May 3 and June 5 seeding dates were counted 22 and 19 days after planting, respectively. One week before harvest a uniform 60 cm section of plants in each row was uprooted and bundled in newspaper to keep the heads and roots intact. The plants were stored under cover for evaluation of subcrown internode discoloration. The remainder of the row was cut and threshed for yield using a Vogel plot thresher. Total grain yield was calculated as the summation of the 60cm section plus the remainder of the 3 m row.

Data Analysis

The data were analyzed in two ways. In the first, the yield from the inoculated row was calculated as a percentage of the control row. In the second method, the controls were treated as a fifth treatment in addition to the four inoculation methods. The single value from comparison of paired rows can be used to find differences among inoculation methods since each inoculated row is compared to its control row that has been treated in a similar fashion except for the absence of the pathogen. If it is assumed that the control rows act in a similar fashion, then the mean of the four non-inoculated rows can be used as a fifth treatment for comparison to the four inoculation methods with C. sativus. This will be referred to as the overall control. Percentages are used in the first case, and absolute values in the second.

Results and Discussion

Plant emergence was not different for either seeding dates or cultivars with approximately 75% emergence of the 150 seeds planted per 3 m row. Differences did occur as the result of inoculation. Both infested oats and infested straw added to the furrow decreased the plant emergence of the test cultivar by 11% and 4%, respectively (Table 1.1). Use of infested oats was responsible for a 11% reduction in emergence. Although Sallans (46) recommended soaking the seed in a conidial suspension for a seedling blight test, this method was not responsible for

Table 1.1. Effect of four methods of inoculation with Cochliobolus sativus on mean plant emergence, yield, and 1000 kernel weight (Kwt) of four barley cultivars planted on two dates at Bozeman, Montana 1979.

Parameter	Emergence	Yield	1000 Kwt
	% of Control		
Seeding Date[2/]			
May 3	99.7 a[1/]	92.2 a	101.0 a
June 5	98.4 a	114.1 b	99.0 a
Cultivar[3/]			
Bonanza	103.0 a	110.0 b	97.5 a
Betzes	101.0 a	108.0 b	101.0 a
Galt	97.1 a	96.6 a	101.0 a
Centennial	95.5 a	97.0 a	101.0 a
Inoculation Method[4/]			
Infested Oats	89.3 a	95.7 a	99.6 a
Infested Straw	96.4 b	98.6 b	101.0 a
Conidial Suspension	104.0 c	114.0 c	100.0 a
Infested Oats and Mounding	106.0 c	105.0 d	99.3 a

1/ $P \leq 0.01$ Column means within seeding date, cultivar, or inoculation method followed by the same letter are not significantly different using Student Newman Keul's (Stu.N.K.) range test. See Appendix 2 for error mean square (EMS) and degrees of freedom (df).

2/ Averaged across all cultivars and inoculation methods.

3/ Averaged across seeding dates and inoculation methods.

4/ Averaged across seeding dates and cultivars. See text for explanation of inoculation methods.

a stand different from the overall control (Table 1.2). The mounding of soil over the seed furrow, for inoculated and control rows, substantially improved emergence of the test cultivars (Table 1.3). Confusion may arise as to why the stand of plants grown in the presence of infested oat kernels was higher than that of the overall control (Table 1.3). The overall control is an average of the four non-inoculated rows, three of which were shallow planted and one was treated with soil mounded over the furrow. Since the three other inoculation methods resulted in stand reduction as compared to the overall control, the soil mounding must have had an effect. The benefits of deep planting for uniform stand establishment appear to outweigh those of possible reduction in severity of CRR due to shallow seeding (34).

Over all the treatments and cultivars, the yield from the inoculated compared to non-inoculated rows was 8% lower in the early seeded plots. However, in the late seeded plot, the yield of inoculated rows was 14% higher as compared to non-inoculated rows (Table 1.1). A slight reduction in yield was expected in early seeded inoculated rows since they were presumably exposed to the pathogen for a longer period of time (60). It is difficult to explain the increase in yield of inoculated versus non-inoculated rows for all inoculation methods and cultivars planted on June 5 (Table 1.1). Delayed seeding for up to 10 days was reported to reduce severity of CRR (4). Sallans and Tinline reported increased yields from early infections of C. sativus if the

Table 1.2. Effect of four methods of inoculation with *Cochliobolus sativus* on the absolute mean values[1/] for plant emergence, yield, and 1000 kernel weight (Kwt) of four barley cultivars planted on two dates at Bozeman, Montana 1979.

Parameter	Emergence	Yield	1000 Kwt
	no.	g	g
Seeding Date[2/]			
May 3	110 a	486 a	35.4 a
June 5	115 a	289 b	38.1 b
Cultivar[3/]			
Bonanza	115 a	346 a	33.2 a
Betzes	107 a	414 b	38.5 b
Galt	117 a	418 b	34.1 a
Centennial	113 a	371 a	41.0 c
Inoculation Method[4/]			
Infested oats	104 a	376 a	36.5 a
Infested straw	108 a	365 a	37.3 a
Conidial suspension	113 b	395 b	36.4 a
Infested oats + soil mounding	124 c	405 b	36.5 a
Overall Control	116 b	397 b	37.0 a

1/ Number of plants and gram yield per 3m row, gram kernel weight is the mean of two samples of 250 seeds multiplied by four to give 1000 Kwt. $P \leq 0.05$ Column means within seeding date, cultivar, or inoculation method followed by the same letter are not significantly different using Stu.N.K. range test. See Appendix 1 for error mean square and degrees of freedom.

2/ Averaged across all cultivars and inoculation methods.

3/ Averaged across seeding dates and inoculation methods.

4/ Averaged across seeding dates and cultivars. Average of four non-inoculated control rows used as a fifth inoculation method, called Overall Control.

Table 1.3. Effect of four methods of inoculation with Cochliobolus sativus on absolute mean values for plant emergence of four barley cultivars planted on two dates at Bozeman, Montana 1979.

Inoculation Methods[2/]	Number of Plants[1/] Bonanza	Betzes	Galt	Centennial	Mean[4/]
Early Seeding May 3					
1) Infested oats	98	99	104	105*	102*
2) Infested straw	100	94*	102	109	101*
3) Conidial suspension	101	110	120	117	112
4) Infested oats with soil mounding	127*[3/]	120	123	125	124*
5) Overall control	109	108	115	121	113
Late Seeding June 5					
1) Infested oats	115	97	116	102	108*
2) Infested straw	119	109	113	116	114
3) Conidial suspension	127	109	128	96	116
4) Infested oats with soil mounding	131	119	124	122	124*
5) Overall control	122	109	126	115	118

[1/] Number of plants that emerged per 3m row of four replications, 150 seeds per row.

[2/] See text for explanation of inoculation methods.

[3/] $t \leq 0.05$ Column means within each cultivar are compared to the overall control mean by least significant test (LSD) = 13, df 96.

[4/] $t \leq 0.05$ Column means among inoculation methods for all cultivars are compared to the overall control mean by LSD = 4.6, df 96.

environmental conditions were favorable for barley growth (48). Verma has reported that the number of fertile tillers is the yield component most affected by CRR (61). Since infection of the crown region could affect the formation of tiller buds (29), perhaps the plants within the inoculated rows, although producing fewer number of tillers, were allocating the mineral and water resources to the 1-2 main fertile tillers. On the other hand, plants within the non-inoculated rows were continuing to produce excess leaf material in the form of late tillers, thereby diverting some minerals and nutrients that would otherwise go into filling the primary fertile tillers. In comparison then, inoculated rows would produce greater yield than the control rows for the late planting. But as a means of CRR control, late seeding of up to 30 days is unlikely to be acceptable to growers since the grain yield produced is much lower than that for early seeding, e.g., 289 g versus 486 g per 3 m for late versus early seeding, respectively (Table 1.2).

The overall yield response of inoculated Bonanza and Betzes compared to their respective controls was an increase of 11% and 8%, respectively. This differed from that of Galt and Centennial in which the inoculated rows had an overall yield reduction of 3% relative to their non-inoculated controls (Table 1.1). Piening observed under conditions of natural inoculum in Canada, that the grain yield of Bonanza was highest, Betzes was intermediate and Gateway was the least (42). Gateway is susceptible to CRR, and both Gateway and Galt have the com-

mon parent, Newal, in their background. This may explain why Galt in my tests suffered a slight yield reduction. Screening cultivars on the basis of yield response to infection by C. sativus may not always increase the level of resistance to CRR but it would provide an indication of a cultivar's ability to respond to this particular stress.

With the four inoculation methods, yield was consistently lower for the early seeding as compared to the control (Table 1.4). Utilizing either infested oats or straw in the furrow, the reduction in yield may be attributal in part to the reduction in plant emergence and subsequent infection. If we subtract the number of plants that emerged as a result of both methods from the overall control, e.g., 113 minus 102, (Table 1.3) then 11 plants were lost to seedling blight. The mean yield using these same two methods was 459 g and the emergence was 102 plants giving 4.5 g per plant. If we assume no competitive interaction among plants, then the 11 plants may have yielded 50 g of additional grain. But the average yield for both methods was 459 g as compared to 529 g for the control, for a yield loss of 70 g. This would suggest a 20 g grain loss due to subsequent infection and 50 g grain loss to the initial seedling blight. The method using a conidial suspension resulted in a yield of 490 g, or 39 g less than the control. This method did not produce a significant plant reduction as compared to the control, and the 39 g yield loss can be attributed to both seedling and mature plant infections. Infections subsequent to seedling blight resulted in yield

Table 1.4. Effect of four methods of inoculation with Cochliobolus sativus on the absolute mean values for yield of four barley cultivars planted on two dates at Bozeman, Montana 1979.

Inoculation Methods[2/]	Gram Yield[1/] Bonanza	Betzes	Galt	Centennial	Mean[4/]
Early Seeding May 3					
1) Infested oats	403	529	497*	428*	464*
2) Infested straw	393*[3/]	486*	511*	428*	454*
3) Conidial Suspension	453	503	532*	477	490*
4) Infested oats with soil mounding	464	514	532*	455*	491*
5) Overall control	462	544	599	510	529
Late Seeding June 5					
1) Infested oats	246	320	291	290	287*
2) Infested straw	244	315	292	251	275
3) Conidial suspension	267	311	309	310	299*
4) Infested oats with soil mounding	312*	348*	331	286	319*
5) Overall control	224	273	290	280	267 (289)

[1/] Mean grain yield per 3m row of four replications.

[2/] See text for explanation of inoculation methods.

[3/] $t \leq 0.05$ Column means within each cultivar are compared to the overall control mean by LSD = 52, df 96.

[4/] Column means among inoculation methods, for all cultivars, are compared to the overall control mean by LSD = 18, df 96.

losses of between 4% and 7% (20 g and 39 g/529 g x 100). This compares favorably to yield losses of barley, as estimated by the Canadian Disease Survey (4% to 10.7%), in naturally infested soil, based upon the yield of clean plants in mixed stands with infected plants (56).

The 1000 kernel weight of grain from inoculated rows as compared with that from their respective non-inoculated control row was not different across seeding date, cultivar, or inoculation method (Table 1.1). Absolute values for early seeding showed lower kernel weights (35.40 g), than for later seeding (38.08 g). The six row cultivars, Bonanza and Galt, had lower kernel weights (33.24 g and 34.12 g, respectively) than the two row cultivars, Betzes and Centennial (38.5 g and 41.00 g, respectively). None of the four inoculation methods significantly affected the kernel weight as compared to the overall control (Table 1.2).

Problems arose with trying to sow the seed deeply to insure development of a long subcrown internode. Both a compacted seed bed and a lightweight tractor and seeder resulted in relatively shallow seeding. Few plants had sufficiently long subcrown internodes for the assessment of disease reaction based on the percent discoloration of this tissue.

Conclusions

Maximum infection and yield reduction occurred with early seeding and C. sativus infested oat kernels sown in the same furrow as seed of the test cultivar. This method did not result in substantial plant per row variability and yet uniform infection was assured. There were no inoculation by cultivar interactions that were significant, indicating that Bonanza, Betzes, Galt, and Centennial reacted in a similar fashion to each of the four inoculation methods. Betzes and Bonanza, however, yielded more in the inoculated rows as compared to their non-inoculated control rows. Although the total grain yield was reduced using either infested oats or straw, the ease of handling oat kernels as opposed to pieces of straw in large field plots makes the former method the one of primary choice. Kernel weight does not appear to be affected by CRR but no data were collected on number of fertile tillers and number of kernels per head to suggest which yield component(s) was responsible for the yield reduction due to C. sativus infection.