NATURE AND INHERITANCE OF ERGOT (*CLAVICEPS PURPUREA* [FR.] TUL.) SUSCEPTIBILITY IN *TRITICUM TIMOPHEEVI* (ZHUK.) X *SECALE CEREALE* (L.) AND *TRITICUM TIMOPHEEVI* (ZHUK.) X *TRITICUM DURUM* (L.) HYBRIDS

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Philip John Krakar

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A dissertation submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

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ABSTRACT (OVERALL)

Krakar, Philip John, Ph.D., The University of Manitoba, January, 1979. Nature and Inheritance of Ergot (*Claviceps purpurea* [Fr.] Tul.), Susceptibility in *Triticum timopheevi* (Zhuk.) x *Secale cereale* (L.), and *Triticum timopheevi* (Zhuk.) x *Triticum durum* (L.) Hybrids.

Major Professor: Dr. E.N. Larter

Triticale (X *Triticosecale* Wittmack) is susceptible to ergot (*Claviceps purpurea* [Fr.] Tul.), while *Triticum timopheevi* (Zhuk.) possesses genes governing resistance to this fungus. Five ergot resistant *Triticum timopheevi* accessions and one rye (*Secale cereale* L. cultivar UC 90) were used to produce F_1 hybrids and amphidiploids to study the expression of *timopheevi* ergot resistance when it is combined with the rye genome. The ergot resistance levels of the *timopheevi* accessions were not expressed in the wheat x rye hybrids and amphidiploids when sclerotial frequency, sclerotial size, honeydew, and disease indices were examined using nonparametric rank comparisons.

In a second part of this continuing study, combining abilities for ergot susceptibility were examined in the F_1 of *T. timopheevi* x *S. cereale* and *T. timopheevi* x *T. durum* crosses. Specific combining ability effects occurred in data of the *T. timopheevi* x *S. cereale* crosses inoculated with the R3A isolate. Both general and specific effects were obtained for sclerotial frequency and

total sclerotia weight when the *T. timopheevi* x *T. durum* hybrids were inoculated with M15A conidia, while only general combining abilities were obtained at the 5% level for sclerotial frequency and total sclerotia weight when R3A conidia were used for inoculations.

The isolates, male parents, and female parents were assessed in the following manner. The M15A and R3A isolates were compared with a paired-t-test and found to parasitize the various crosses differentially. The effects of the rye and durum males were determined with t-tests and no one rye or durum could be recommended for use with all *timopheevi* accessions. Lastly, Tukey's w-procedure (honestly significant difference procedure) was performed and the 4B288 *T. timopheevi* accession was indicated as the better accession to cross with the line 127 rye and Carleton durum. Consequently, the 4B288 x line 127 cross was recommended for further studies.

FOREWORD

This thesis is written in a manuscript style approved by the Plant Science Department of the University of Manitoba. The manuscripts follow the style of the Canadian Journal of Plant Science in order that they can be submitted to the journal with a minimum of modification.

INTRODUCTION

Ergot, a disease caused by the fungus *Claviceps purpurea* (Fr.) Tul., attacks members of the family Gramineae (Seaman, 1971; Walker, 1969). Of the cultivated cereal species attacked, rye (*Secale cereale* L.) is generally considered to be the most susceptible due to its outcrossing nature (Walker, 1969). The florets of other cereals such as spring wheat (*Triticum aestivum* L. em Thell.) and barley (*Hordeum vulgare* L.) do not remain open during flowering to the same extent as rye and, therefore, have morphological resistance (Walker, 1969). Triticale (X *Triticosecale* Wittmack), although naturally self-pollinating, has outcrossing characteristics (Yeung and Larter, 1972) resulting in the tendency of florets to remain partially open for an extended period of time. Consequently, morphological resistance does not operate in triticale as it does in other self-pollinating species so that this species can be parasitized by the ergot fungus. Once the ergot pathogen establishes itself in triticale, a sclerotium is produced in place of the host's seed.

The sclerotia produced by the ergot fungus are toxic to both monogastrics and ruminants (Campbell and Burfening, 1972; Purchase, 1974; Ingalls and Phillips, 1971). A level of only 2% ergot sclerotia by weight in flour is sufficient to cause epidemics of ergotism in human populations (Kingsbury, 1964). The type of

ergotism produced depends on the rate at which the animal consumes the sclerotia; a rapid ingestion causes convulsions while a slow consumption results in gangrene. In addition, a level of 0.53% sclerotial contamination by weight in the diets of mice and gilts can result in abortion (Campbell and Burfening, 1972), while a 0.07% level in the diets of calves can reduce growth rates (Ingalls and Phillips, 1971).

In western Canada the accepted tolerance level of ergoty grain is only 0.25% sclerotia by weight (Riley, 1973). Many grain importing countries impose even a lower tolerance limit and refuse to import grain that has more than 0.04% ergot sclerotia by weight (Riley, 1973). Unfortunately, it is not practical to achieve either of these tolerance levels by mechanically separating the ergot sclerotial bodies from the grain. Thus, in order to meet these low tolerance levels, it would be desirable to introduce some type of resistance into susceptible crops such as rye and triticale. It would also appear that the only resistance capable of restricting sclerotia to the levels permitted in rye and triticale is a physiological resistance which is operative before fertilization.

Physiological resistance to *C. purpurea* has been located in certain cultivars of spring wheat (Platford and Bernier, 1976). Within the spring wheat accessions of the University of Manitoba, the best physiological resistance is that found in *Triticum timopheevi* Zhuk. (Bernier, 1976). An effort was made, therefore, to transfer this resistance into wheat-rye (triticale) amphidiploids.

To be of value in hexaploid triticale, the *T. timopheevi*

resistance must be expressed in the presence of the genomes of wheat (A,B) and rye (R). At the beginning of the study little was known concerning these effects. Consequently, a study was initiated to determine the influence of the R genome on the *timopheevi*-type resistance, followed by a second study for the purpose of obtaining information on ergot resistance in hybrids of *T. timopheevi* x *S. cereale* and *T. timopheevi* x *T. durum*.

LITERATURE REVIEW

Because of the paucity of literature concerning the problem of ergot in triticale, this literature review will consider general but pertinent aspects of the pathogen and host, *Claviceps purpurea* (Fr.) Tul. and *Triticum timopheevi* Zhuk., respectively. In relation to the pathogen, the following areas will be discussed: (1) the life cycle, (2) host range, (3) types of ergot resistance, (4) methods of estimating physiological resistance, and (5) inheritance in intraspecific and interspecific crosses. In regard to the host *T. timopheevi*, the following aspects will be considered: (1) the genomic constitution of tetraploid *timopheevi*, (2) the formation and use of intraspecific and interspecific crosses involving *timopheevi*, and (3) hexaploid *timopheevi*. The genomic constitution of *timopheevi* is known to differ from that of other wheats. Consequently, for the purpose of clarity, the tetraploid *timopheevi* will be designated genomically as AAGG throughout this literature review and study.

The Pathogen, *Claviceps purpurea* (Fr.) Tul.

Life Cycle of the Pathogen

Claviceps purpurea overwinters as sclerotia in the soil or mixed with the grain that is planted the following season. After a period of cold temperature the resting stage is completed and

when higher temperatures return, germination can occur. Germination initiates the sexual stage of the fungus. One to several stromata are produced which are composed of a stipe (15 to 30 mm long) and a stroma bearing the perithecia (Walker, 1969; Bove, 1970). The perithecia themselves are embedded within the stroma so that only the ostioles protrude from the surface (Moore-Landecker, 1972). It is in these perithecia that many long, narrow asci are produced, each of which produces eight needle-shaped ascospores.

At a subsequent stage of development, each ascospore is extruded or forcibly ejected (Colotelo and Cook, 1977). If the ascospore lands or falls in a floral cavity of a susceptible host, it germinates and mycelia penetrate the ovary wall near the base of the ovule (Kirchhoff, 1929). For two or three days the fungus grows intercellulary in the outer integuments of the ovary, then intracellulary for another four or five days (Campbell, 1958). Finally, it penetrates the integument barrier and a host-parasite interface is established between the fungal thallus and the cereal flower rachilla (Mower and Hancock, 1975b).

A sphacelical or conidial stage ensues and during this stage conidia are produced in a sticky exudate called honeydew. The honeydew can be spread to other florets by insects or by simply dripping onto lower florets. Once spread to these susceptible florets, the conidia can initiate secondary infections.

Mower and Hancock (1975a) propose that the honeydew itself is produced by the conversion of host sucrose to mono, di- and oligosaccharides by fungal enzymes. During this time, water is

lost through evaporation from the surface of the honeydew and because of the heavy demand for sugar at the host-parasite interface, an osmotic potential is created. The interface becomes a sink which draws the sucrose into the diseased area (Mower and Hancock, 1975a).

The honeydew stage always develops prior to the formation of the sclerotia (Mower and Hancock, 1975a). At some stage, the fungal hyphae compact and form sclerotia which are either harvested with the grain or fall to the ground. They then pass through a critical dormant period and are again ready to germinate, thus completing the life cycle of the fungus.

Fungal Host Range

The host specificity of a parasite is an important component in the control of any plant disease in the field. The greater the number of hosts that the fungus can parasitize, the greater the inoculum load that is available for overcoming resistance. *Claviceps purpurea* has a wide host range, attacking many genera in the family Gramineae. Because of this relationship, various studies have been carried out to determine the host specificity of this fungus. Five physiological races were initially identified by Stager (1903, 1923), Mastenbroek and Oort (1941), and Baldacci and Forlani (1948). Loveless (1971) suggested these would be better termed *formae speciales*. The *formae speciales* were initially distinguished primarily on the basis of their ability to attack *Secale cereale* L. and *Lolium perenne* L. differentially (Dickson, 1956; Sprague, 1950; Platford, 1976). Thus, the *formae speciales* that attacked *Secale*

cereale L. also attacked *Triticum timopheevi* L. em Thell., *Festuca elatior* L., *Bromus sterilis* L., but not *Lolium perenne* L.

Campbell (1957) reported that Bekesy was able to infect *Lolium perenne* L. with the *formae speciales* from rye, and tested all the previous methods of inoculating that had been used in determining the host-parasite specificity of *Claviceps purpurea* (Fr.) Tul. The four methods he tested were: spraying heads with a conidial suspension, dipping the heads into a spore suspension, dropping the spore suspension into the florets while holding the glumes apart, and injecting conidia into the florets. Using these methods, Campbell (loc cit) was able to cross-inoculate various hosts with all but one of 421 isolates. From his results he felt there was no conclusive evidence to suggest the existence of *formae speciales*, but rather that the method of inoculation was the important factor in obtaining infection.

Loveless (1971), and Loveless and Peach (1974), on the other hand, support Stager's differentiation of *Claviceps purpurea* into *formae speciales*. They demonstrated that conidial length and ascospore size are controlled by the fungus independent of the host, whereas sclerotial size was governed by the host. By examining the conidia and ascospores of a wide range of hosts, they were able to demonstrate a difference in size between conidia and ascospores. Using these differences as criteria for the differentiation of *formae speciales*, the results were similar to those obtained when the virulence of *Claviceps purpurea* was used as the criterion.

Different authors have suggested various reasons for the

apparent host specialization. Campbell (1957) indicated that there was no host specialization and that the previous results were due to the method of inoculation used in the various studies. Peach and Loveless (1975) indicated that the method of inoculation influenced the degree and presence of infection and that artificial inoculation, which circumvents certain natural barriers to resistance, does not stimulate infection under field conditions. Consequently, they favored using the spray method as it more closely stimulates natural infection. Platford (1976) indicated that neither the virulence of the isolates nor the inoculum concentration had been considered in previous studies and both of these factors could be important. Ratanopas (1973), for example, was able to show that there were differences in the virulence of isolates, while Platford and Bernier (1976) demonstrated that inoculum concentration had an effect on infection levels obtained. However, little attention has been devoted to the influence of environmental conditions on infectivity. The environmental conditions could be responsible for the lack of uniformity of results between investigations. Because of this fact, the host specialization of *C. purpurea* has not been firmly established.

Types of Ergot Resistance

In many plant species, resistance to ergot is clearly a function of escape from infection. If the florets are tightly closed, inoculum is unable to enter the floret and initiate infection. Conversely, the degree of infection is a function of the degree and

time of floral openings. Increased sterility in male sterile barleys (Puranick and Mathre, 1971; Cunfer et al., 1975), in male sterile wheats (Darlington and Mathre, 1976), in interspecific wheat hybrids (Waterhouse, 1953), and in cross pollinating rye (Abe and Kono, 1957), contributes to a greater incidence of ergot infection. Any reduction in either the degree or length of time of floral opening in these types of plants reduces ergot incidence. Consequently, increased fertility which reduces floral opening time has resulted in a reduced infection rate in triticale and rye (Larter, 1974; Sosulski and Bernier, 1975).

Date of flowering in relation to ascospore release or production of conidia can also affect ergot incidence. The occurrence of ergot in fall rye grown on the prairies is usually low as it flowers before the main ascospore release of *C. purpurea* (Sosulski and Bernier, 1975). Mantle and Shaw (1976) have shown that in southern England, ascospores, which originated from a sclerotium produced on wheat, did not infect wheat. Rather, the ascospores initially infected black-grass (*Alopecurus myosuroides*), and from this they spread to the wheat crop as a secondary conidial infection. Consequently, even though ascospore release had declined over 50% by the time the wheat was reaching anthesis, there was adequate inoculum present in the field to infect wheat.

The fertilization of the cereal flower appears to preclude its infection by the ergot organism. Puranik and Mathre (1971) found that within four days after fertilization, barley ovaries exhibited a reduction in susceptibility, whereas unfertilized florets required

10 days to exhibit a comparable reduction in susceptibility. Cunfer et al. (1975) were able to show a decrease in infectivity of fertilized barley florets within hours after pollination. Darlington and Mathre (1976) found resistance to ergot infection in the wheat cultivars Chris, Pembina, and Sheriden increased within 30 minutes following pollination. Ratanopas (1973) noted fertilization affected various aspects of ergot infection. He found that both the production of sclerotia and the amount of honeydew were reduced while the proportion of partial infections and aborted florets increased as a result of fertilization in the cereal cultivars, Kenya Farmer and Manitou wheat, Rosner triticale, Conquest barley, and Prolific rye.

Physiological resistance to ergot has been found in the durum wheat cultivar, Carleton, and in the hexaploid wheat, Kenya Farmer (Platford and Bernier, 1970). This resistance was expressed as a reduction in both the number of sclerotia and the amount of honeydew that the cultivars produced. Darlington and Mathre (1976) indicated that the cultivars Chris and Pembina have some resistance, but less than Kenya Farmer. Spring wheat has been found to possess the best ergot resistance of all cereals tested (Platford and Bernier, loc cit).

Methods of Estimating Physiological Resistance

In order to detect whether physiological resistance is present, it is necessary to have some method of estimating the infection on hosts differentially. Many of the early studies used only the

presence or absence of sclerotia as the means of estimating the degree of ergot incidence (Stager, 1923; Campbell, 1957). This method, however, may not be sufficiently sensitive to identify all resistance genes that may be present in the host.

Futrell and Webster (1965) used a more sensitive measure of the occurrence of sclerotia whereby they determined the number of florets infected and expressed this as a percent of the total florets per spike. Waterhouse (1953) used the weight of a given number of sclerotia per plant line as an estimate of resistance.

Schmidt and Lucken (1976) compared three types of estimates of disease reactions. Their estimates were based on the number of sclerotia per spikelet, the weight of sclerotia per spikelet, and the size of the sclerotia. The size of sclerotia was determined by passing them through screens of varying sizes. They found that sclerotia number provided the more precise measurement of resistance. The partially infected ovaries which failed to develop into typical sclerotia were included in the estimates of sclerotia number and, as these workers indicated, partial infections may be a useful form of resistance.

Platford and Bernier (1976), and Ratanopas (1973) used the number of sclerotia, size of sclerotia (rated in relation to normal seed size), partially infected ovaries, and honeydew production in estimating physiological resistance. They found each of these parameters had their own individual reactions and should be examined separately. These components were used to formulate a disease index rating that classified the disease reaction from immunity to highly

susceptible (Platford, 1976; Ratanopas, 1973).

Noticeable in all these studies is the fact that no researcher has used the weight of sclerotia produced on a given number of florets per head as a measure of resistance. If this method was used, it would be a measure analogous to the index system of Ratanopas (1973) as the measurements would reflect the effect of both size and number of sclerotia. This system would also have the advantage in that it would not be a rating but rather a quantitative weight measurement.

Platford (1976) has studied the possibility of utilizing a coleoptile inoculation test to determine the resistance reaction of rye, spring wheat, triticale, oats, and barley. He found that such a test may be of value in screening for ergot resistance in the first three mentioned species.

Inheritance of Ergot Resistance in Intraspecific and Interspecific Crosses

Robinson (1960), working with resistant and susceptible hybrids of sugar cane, found that resistance to *C. purpurea* was inherited recessively.

Schmidt and Lucken (1976) crossed six wheat cultivars in diallel, three of which exhibited resistance to ergot, the remaining three susceptible to ergot. By analyzing the data by Griffing's method, they found general combining ability accounted for most of the variability for the number and weight of sclerotia per spikelet.

Galstjan-Avanesjan (1967) tested progenies from wheat-agropyron and wheat-rye crosses for ergot resistance and found resistance to

be recessive in certain parents and dominant in others. It was concluded from the results that resistance was an unstable quantitative character.

Riley (1973), using F_1 monosomic analysis and assuming resistance genes to be homoeoallelic to susceptible genes in the cultivar, Chinese Spring (i.e., homologous genes in different genomes; Feldman, 1976), found that part of the resistance of *T. timopheevi* (Manitoba accession no. 4B289) was conditioned by genes on chromosome 3G. Resistance was inherited as a dominant trait when crossed to some tetraploid wheats, but recessive when crossed to the hexaploid, cv. Chinese Spring. This study was inconclusive because the aneuploid stocks had not been previously tested for monosomic shift.

Riley (1973) also studied ergot resistance in the durum wheat cultivar, Carleton. Assuming genes were homoeoallelic, he found that resistance was conditioned by gene(s) on chromosome 1B and 3B. Furthermore, he demonstrated this resistance to be inherited as a recessive trait when crossed to both the hexaploid wheat, Chinese Spring and the tetraploid, Stewart 63.

Similarly, Platford (1976), using Carleton-Chinese Spring monosomic F_1 hybrids to study the location of genes governing resistance in Carleton, found them to be located on chromosome 1B. He, too, assumed resistance as homoeoallelic to susceptibility in Chinese Spring. Because it is possible that susceptibility can be caused by interchromosomal gene action rather than intrachromosomal homoeoallelic action, the results of these studies must be viewed with discretion.

Platford (1976), using the Kenya Farmer-Chinese Spring substitution series, found the ergot resistance of Kenya Farmer to be located on chromosome 6B. There was no indication that shift had occurred when he tested the monosomic 6B line with a race of rust; the resistance to which is known to be controlled by a gene located on chromosome 6B.

The genetic inheritance of ergot resistance in progenies from Kenya Farmer x Chinese Spring and Carleton x Stewart 63 hybrids was studied using F_1, F_2, and F_3 populations (Platford, 1976). Disease reaction appeared to be controlled by two recessive genes in Kenya Farmer and by two dominant genes in Carleton. There was also a suggestion that sclerotia frequency, sclerotia size, and honeydew production were controlled by separate genes.

Waterhouse (1953) inoculated both rye and sterile *T. timopheevi* x *H. vulgare* F_1 hybrids with ergot conidia. He found no significant differences in weight of 100 sclerotia harvested from each of the populations. If *timopheevi* possessed genes for resistance, they were expressed as recessives.

Riley (1973) was able to successfully grow three sterile *T. timopheevi* x *S. cereale* hybrids. He inoculated the three plants with *C. purpurea* and found one to be susceptible to ergot even though the *T. timopheevi* female parent was ergot resistant.

The Host, *Triticum timopheevi* Zhuk.

Triticum timopheevi is a tetraploid wheat that is indigenous to western Iran, northwestern Iraq, eastern Turkey, Armenia, and

Transcaucasia (Feldman, 1976). Cultivated forms are grown in Armenia and Transcaucasia today (Feldman, 1976). Many researchers consider *T. timopheevi* useful only as a source of resistance rather than as a cultivated crop because of its many poor agronomic characteristics. Furthermore, *timopheevi* has a different genomic constitution than *T. durum* and *T. aestivum* which creates difficulties in the interspecific transfer of resistance. The taxonomic differences that exist between these wheats as well as hypotheses regarding the origin of these differences have been examined in several cytogenetic studies.

The Genomic Constitution of Tetraploid *Triticum timopheevi*

Triticum timopheevi is compatable with other tetraploid wheats, but the F_1 hybrids are partially asynaptic and highly sterile (Feldman, 1976). Because of this phenomenon, Lilienfeld and Kihara (1934) designated *T. timopheevi* genomically as AAGG (Bozzini and Giorgi, 1969). Kostoff (1937), on the other hand, designated *T. timopheevi* as AABB because of the affinity of the B- and G-genomes. He was not convinced that there were sufficient differences in chromosome homologies to warrant a distinct designation.

Sachs (1953) indicated that the sterility observed in these hybrids was chromosomal in origin. He hypothesized that the small cryptic structural differences (i.e., many small non-homologous chromosomal segments) which were present would allow bivalents to form but would still cause sterility.

Wagenaar (1961, 1966), on the other hand, believed that

sterility in a *timopheevi*-tetraploid wheat hybrid was due to what he termed "asynaptic genes". He proposed that a *T. timopheevi* x *T. turgidum* F_1 hybrid was heterozygous for these genes. This condition could cause imperfect pairing and chiasmata formation which in turn would result in sterility. If the F_1 hybrid was then doubled, however, the amphidiploid would be homozygous as in the tetraploid wheats which would encourage normal pairing and chiasma formation. This, in turn, would result in the amphidiploid being fertile. Any chromosomal structural differences that were present would have arisen after the synaptic genetic system had formed the sterility barrier between the *timopheevi* and the other tetraploid wheats.

Feldman (1966a) crossed Chinese Spring telocentrics to a *T. timopheevi-A. squarrosa* amphidiploid and studied 19 of the 28 chromosome arms of *T. timopheevi*. He found that pairing in the A-genome was higher than that between the G- and B-genomes. Multivalent associations were found involving the B- and G-genomes, representing at least five translocations. He, therefore, concluded that there were large chromosomal differences differentiating the B from the G genome. These, he designated as B^tB^t. He also noted that no conclusion could be drawn as to whether the G-genome was derived from the B-genome, the B- from the G-genome, or whether the G and B evolved from a common progenitor.

After studying the karyotype of various tetraploid wheats, Bozzini and Giorgi (1969) also concluded the tetraploid *timopheevi* group was separated by gross chromosomal structural differences.

Superimposed on these structural differences were factors causing cytoplasmic male sterility.

Rees and Walters (1965) found less DNA in *timopheevi* than they did in durum species. They concluded from this that the G- and B-genomes must differ in their DNA contents as they assumed the A-genome, which is common to both species, was identical in DNA content. However, it is possible that the A genomes of the two wheats may not be identical.

Zohary and Feldman (1962) proposed the following hypothesis to explain the divergence between the *timopheevi* and durum wheats. Based on the two facts that (1) the A-genomes pair better than the B- and G-genomes, (2) both *timopheevi* and durum have a diploidization mechanism, they proposed that the A-genome acted as a pivotal genome around which the G- and B-genomes diverged. The A-group provided the needed initial fertility in crosses to enable both chromosomal and genic changes to occur. Once they had diverged to the point where sterility occurred, it was hypothesized that genic changes occurred in the common A-genome of *timopheevi* which restored fertility. If this assumption is valid, it should be possible to show the A-genomes in *timopheevi* and durum are genically different.

Johnson et al. (1967) and Johnson (1967), subjecting seed extracts to gel electrophoresis found such differences in the genetic make-up between *timopheevi* and durum. They found two albumin bands in *timopheevi* and four in durum that were not in common, while five bands were common to both species. In these studies, there also appeared to be differences in the slow moving gliadin bands. At least two of these

differences could be due to differences in the A-genome, lending support to the hypothesis of Zohary and Feldman (1962).

Shands and Kimber (1973) suggested that the G-genome is similar to the S-genome of *speltoides*. Feldman (1976), on the other hand, postulated that the common progenitor of the G- and B-genomes is diploid bicourne (S^b).

The Synthesis and Use of Intraspecific and Interspecific *T. timopheevi* Crosses

Various attempts have been made to transfer disease resistance from *T. timopheevi* to *T. aestivum*. One such report is that of Allard (1949) in which he reported an attempt to transfer the resistance of *timopheevi* to *T. aestivum* by backcrossing the sterile F_1 hybrid to *T. aestivum*. He found that each successive backcross improved pairing and fertility, so that by the third backcross he had obtained a 56% seedset. By the fourth backcross he could no longer observe *timopheevi* characteristics. However, because of the variability within populations, it appeared that the influence of *timopheevi* germplasm was still being expressed. The expression of disease resistance was likewise variable in his study. The full complement of resistance to stem rust (*Puccinia graminis* Pers. f. sp. *tritici* Eriks. and Henn.) was expressed in the *T. timopheevi* x *T. aestivum* cross while resistance to leaf rust (*Puccinia recondita* f. sp. *tritici* Rob. ex. Desm.) was only partially expressed. In spite of the problems involved, Allard indicated it is possible to transfer into *T. aestivum* some of the disease resistance which is expressed by *T. timopheevi*.

Bell and Lupton (1955) reported results similar to those of Allard. They found that resistance to stripe rust (*Puccinia striiformis* West.) was not expressed in a *T. timopheevi* x *T. ovata* hybrid. Resistance to stem rust was expressed in only some hybrids for certain races while resistance to mildew (*Erysiphe graminis tritici* E. Marchal) was never expressed when a susceptible tetraploid wheat was used. They interpreted the resistance as being inherited as a dominant gene in some amphidiploids, while in others a recessive or a partially recessive gene. In addition to these three types of reactions, they also found transgressive segregation for susceptibility. This they explained on the basis that the two parents each possessed a different mechanism for resistance and that neither of these mechanisms were able to operate in the amphidiploid.

Waterhouse (1953) pollinated 195 *T. aestivum* florets with *T. timopheevi* pollen and obtained 21 seeds. From these he was able to secure three sterile F_1 hybrids with a seedset of 1.5%. When they were inoculated with ergot (conidia), sclerotia were produced. Consequently, the ergot resistance of *T. timopheevi* appeared to be recessive to the susceptibility of *T. aestivum*.

Success in utilizing interspecific crosses for the transfer of *T. timopheevi* disease resistance is difficult to achieve. Kostoff (1937) provided one of the earliest reports of a *T. timopheevi* x *S. secale* cross. He produced two sterile F_1 plants which he analyzed at meiosis. His analysis revealed that up to 21 univalents were present at metaphase 1.

Nakajima (1955) reported the results of crosses of tetraploid *T. timopheevi* to various rye species, namely *S. cereale* L., *S. africanum* Stapf., and *S. montanum* Gus. He obtained a seedset of 0.04%, 22.03%, and 17.12%, respectively, and from this he produced one hybrid plant which lacked pistil formation. Tsunewaki (1974) reports these same data a second time. Sanchez-Monge (1956) indicated that he pollinated 1444 *T. timopheevi* florets with rye pollen and obtained a seedset of 0.3%. In none of these reports, however, are there indications that amphidiploids were produced.

Because of recent advances that have been made, in controlling environments and laboratory techniques, these early studies on interspecific crosses need to be re-examined. Improved embryo culture techniques and more optimal environmental conditions have served to enhance the production of amphidiploids (Kaltsikes, 1974; Taira and Larter, 1978). Moss (1972) obtained seedsets of 38.5%, 23.8%, and 12.9% from *T. timopheevi* Zhuk. x *S. ancestrale* Zhuk.; *T. timopheevi* Zhuk. x *S. cereale* L. (diploid); and *T. timopheevi* Zhuk. x *S. cereale* L. (tetraploid) crosses, respectively. He indicated that the cause of the low number of viable seeds at the tetraploid level occurred as a result of endosperm failure. This, he maintained, was in contrast to the hexaploid wheat-rye cross in which an incompatability barrier was operative between the time the pollen tube penetrated the micropyle and the first division of the fertilized egg and polar bodies.

Hexaploid *timopheevi*

The hexaploid form of *T. timopheevi* var. *zhukovskyi* is genomically designated AAAAGG (or AAAABB). Sallee and Kimber (1976), while studying a *T. timopheevi* var. *zhukovskyi* x *S. cereale* hybrid, observed that seven bivalents were formed. This indicated to them that one of the genomes in *T. timopheevi* var. *zhukovskyi* was duplicated. Johnson (1968), Upadhya and Swaminathan (1963), and Dhaliwal and Johnson (1976), using electrophoresis analysis on seed extracts along with studies on chromosome pairing, have ascertained the duplicated genome to be the A-genome. Because of the genomic constitution of var. *zhukovskyi*, Sallee and Kimber (1976) have termed it an autoallohexaploid.

MANUSCRIPTS

MANUSCRIPT I

Loss of *Triticum timopheevi* resistance to ergot (*Claviceps purpurea* [Fr.] Tul.) in *Triticum timopheevi* x *Secale cereale* hybrids and amphidiploids.

ABSTRACT

Five accessions of *Triticum timopheevi* Zhuk. and one of rye (*Secale cereale* L. cv. UC 90) were used to synthesize sterile F_1 hybrids and their amphidiploids. The five *timopheevi* accessions, the rye parent, the sterile F_1 hybrids, and their amphidiploids were inoculated with *C. purpurea* (Fr.) Tul. in order to study the expression of the *timopheevi* resistance when combined with the rye genome. The full component of the *T. timopheevi* resistance was not found to be expressed in the wheat-rye (triticale) derivatives.

INTRODUCTION

Ergot (*C. purpurea* [Fr.] Tul.) can be a serious problem on triticale (X *Triticosecale* Wittmack) when this crop is grown in temperate regions of the world. Semi-sterility and the outcrossing of the parental rye (*S. cereale* L.) can prolong floret opening and thereby enhance the incidence of ergot in triticale (Yeung and Larter, 1972). The gradual improvement of the fertility of triticale through breeding has greatly reduced, although not completely alleviated the ergot problem (Larter, 1974). Consequently, physiological resistance is needed and is being sought in the triticale breeding program at the University of Manitoba.

Physiological ergot resistance that is expressed before ovule fertilization has been found in certain wheat species (Platford and Bernier, 1970, 1976); the best resistance occurring in the species *T. timopheevi* (Bernier, 1976). A study was initiated, therefore, to determine if the *timopheevi* ergot resistance would be expressed in *T. timopheevi* x *S. cereale* F_1 hybrids and amphidiploids.

MATERIALS AND METHODS

Five lines of *T. timopheevi* Zhuk. (University of Manitoba accessions 4B573, 4B286, 4B288, 4B289, and 6B501) were chosen because of their known resistance to *C. purpurea* (Fr.) Tul. Accession 6B501 is hexaploid (2n=6x=42); the remaining four are tetraploid (2n=4x=28).

Crosses were made using *timopheevi* as the female parent and the open pollinated rye (*S. cereale* L. cv. UC 90) as the male. All fertilized ovules were removed from the maternal parents 12 to 14 days after pollination and the excised embryos were cultured according to the method described by Taira and Larter (1978). Fertile amphidiploids (2n=6x=42) were formed by treating the sterile F_1 plants with colchicine according to the methods of Winkle and Kimber (1976).

Parental material, F_1 hybrids, and respective amphidiploids were grown in a completely randomized design under an 18 hour photoperiod with a minimum light intensity of 7,532 lx. During the artificial inoculation period, the temperature was maintained at $24^{o}C$. Ten florets of each head were inoculated, using a hypodermic syringe, approximately two days before anthesis (Platford and Bernier, 1976). Each floret was injected with 0.02 ml of a conidial suspension that had been diluted to 10^4 conidiospores per ml.

All conidial suspensions used were produced from stalk cultures derived from a single ascospore isolate in order to reduce the

effect of fungal variability on the disease ratings. The isolate was designated as University of Manitoba R3A. This isolate was chosen as it was known to attack *S. cereale* and *T. timopheevi* differentially.

Approximately 30 days after inoculation, disease reaction was indexed according to the system of Ratanopas (1973). Accordingly, sclerotial number was rated as a percent of the 10 florets inoculated. Sclerotial size was rated on a 1 to 3 scale; 1 being smaller than a normal triticale kernel; 2, the same size; and 3, larger than a normal kernel. After rating, a sclerotial size index was calculated using the formula:

$$\frac{\sum_{i=1}^{3} N_i \times R_i}{T \times 3}$$

where i = the size class

N_i = number of sclerotia in the i^{th} size class

R_i = size class multiplier 1, 2 or 3

$T = \sum_{i=1}^{3} N_i$

The occurrence of honeydew was rated as 1, no visible honeydew; 2, honeydew confined within the glumes; 3, honeydew exuding from the florets in small drops; 4, honeydew exuding from the florets in large drops and running down the head. Using these ratings, Ratanopas' Disease Index reaction was determined (Table 1).

The distribution-free Kruskal-Wallis test was used for data analysis (Campbell, 1974; Zar, 1974). This procedure was followed by the distribution-free, multiple comparison of Dunn (Hollander and Wolfe, 1973) to identify those treatments that were significantly different. Non-parametric tests were used because the data were

TABLE 1. Disease reaction caused by *Claviceps purpurea* (Ratanopas, 1973)

Disease reaction	Infection			
	Disease index	Sclerotia size	Frequency of sclerotia	Honeydew
Immune (I)	0	No infection; seed in all florets.	-	1
Very resistant (VR)	1	Abortive reaction (AR) mainly; no sclerotia.	-	1
Resistant (R)	2	AR and sclerotia of size 1 & 2 only.	Not greater than 40%.	1-2
Moderately resistant (MR)	3	Sclerotia mainly size 1 & 2; 1 to 3 sclerotia of size 3.	Not greater than 60%.	1-2
Moderately susceptible (MS)	4	Sclerotia of size 2 & 3.	Not greater than 80%.	3
Susceptible (S)	5	Sclerotia mainly size 3.	Greater than 80%.	4

recorded as ratings and, therefore, not necessarily normally distributed.

RESULTS AND DISCUSSION

The disease reaction of rye was rated as susceptible (Table 1). The tetraploid *timopheevi* wheats ranged from very resistant to resistant, whereas the hexaploid wheat accession ranged from very resistant to moderately resistant. The sterile F_1 hybrids exhibited the widest range of disease reaction, ranging from resistant to susceptible. Variability in the expression of resistance of sterile F_1 hybrids can possibly be explained on the basis of the heterogeneity that exists within the gametic population of the open-pollinated rye parent. Furthermore, genes governing susceptibility to ergot could be present within the rye genotype. If this is the case, *timopheevi* genes conferring resistance to ergot would not be expressed in all *timopheevi* rye genotypes. At the amphidiploid level there was less variability in the disease expression, with the reaction ranging from moderately susceptible to susceptible. This relatively narrower range of variability could be a result of the limited sample size as amphidiploids from only two of five wheat x rye crosses were available for study.

If the disease expression of hybrids from the various *timopheevi* accessions was compared to that of the respective *timopheevi* and rye parents, some *timopheevi* resistance was found to be expressed at the F_1 level (Table 2). This was also indicated by the fact that the various disease reactions of the F_1 hybrids were

TABLE 2. Significance levels[+] of comparisons of disease components of five parental *timopheevi*, one rye, and the five resulting F_1 hybrids

Comparison[ε]	Heads compared	Sclerotia no.	Sclerotia size index	Honeydew	Disease index
AAGG to AGR	25 to 109	.05	.01	.01	.01
AAGG to RR	25 to 9	.01	.01	.01	.01
AGR to RR	109 to 9	.01	.01	.01	ns

[+]based on significance level determined by Dunn's procedure after the Kruskel Wallis test had been applied to ranked data

[ε]AAGG = *timopheevi* (AAAAGG also included in this), AGR = F_1 hybrid, R = rye

intermediate to those expressed by the *timopheevi* and rye parents.

The Disease Index is the combined product of the three disease components, sclerotia size, sclerotia number, and honeydew formation. In comparisons with rye, the three disease components in the F_1 hybrids (i.e., comparison AGR to RR, Table 2) are significantly different while the overall Disease Index is not significantly different for the two groups. This can be explained on the basis that if any one of the disease components of a plant falls into the susceptible class, the plant is indexed as susceptible; the honeydew component most often has this effect. Because of the large proportion of susceptible plants, there is a loss of significance when compared to the susceptible rye parent.

The rye genome generally induces a reduced expression of *timopheevi* resistance in a *T. timopheevi* x *S. cereale* hybrid. If the two *timopheevi* accessions that are represented in both F_1 hybrid and amphidiploids are studied, there seems to be a difference in the way the rye gamete operates. When comparisons are made between the 4B573 accessions and the F_1 hybrid (AAGG and AGR), the F_1 hybrid and the amphidiploid (AGR and AAGGRR), and the amphidiploid and rye (AAGGRR and RR), no significant differences are found except for sclerotia number between the sterile F_1 hybrid and the resulting amphidiploid (Table 3). When accession 4B288 was used as the female parent, no significant differences in sclerotia number and size were found between the sterile F_1 hybrid (AGR) and the amphidiploid (Table 4). The rye genome, therefore, appeared to be reacting differently when incorporated into the genetic background of the two *timopheevi*

TABLE 3. Significance levels[+] of comparisons of ergot sclerotia number and size, honeydew, and Disease Index when the wheat *Triticum timopheevi* Zhuk. (Manitoba accession 4B573) and the rye UC 90 were used to synthesize hybrids and amphidiploids

Comparison[ε]	Heads compared	Sclerotia size index	Sclerotia no.	Honeydew	Disease index
AAGG to AGR	5 to 23	ns	ns	ns	ns
AGR to AAGGRR	23 to 13	ns	.01	ns	ns
AAGGRR to RR	13 to 9	ns	ns	ns	ns
AAGG to AAGGRR	5 to 13	.01	.01	.01	.01
AAGG to RR	5 to 9	.01	.01	.01	.01
AGR to RR	23 to 9	.01	.01	.01	.05

[+]based on significance level determined by Dunn's procedure after the Kruskel Wallis test had been applied to ranked data

[ε]AAGG = *timopheevi*, AGR = F_1 hybrid, R = rye, AAGGRR = amphidiploid

TABLE 4. Significance levels[+] of comparisons of ergot sclerotia number and size, honeydew, and Disease Index when the wheat *Triticum timopheevi* Zhuk. (Manitoba accession 4B288) and the rye UC 90 were used to synthesize hybrids and amphidiploids

Comparison[ε]	Heads compared	Sclerotia size index	Sclerotia no.	Honeydew	Disease index
AAGG to AGR	5 to 31	.05	.05	ns	ns
AGR to AAGGRR	31 to 8	ns	ns	ns	.05
AAGGRR to RR	8 to 9	.01	.01	ns	ns
AAGG to AAGGRR	5 to 8	.05	.05	.01	.01
AAGG to RR	5 to 9	.01	.01	.01	.01
AGR to RR	31 to 9	.05	.01	.01	.05

[+]based on significance level determined by Dunn's procedure after the Kruskel Wallis test had been applied to ranked data

[ε]AAGG = *timopheevi*, AGR = F_1 hybrid, R = rye, AAGGRR = amphidiploid

accessions. When 4B573 formed the background genotype the level of ergot resistance was reduced with each dose of the rye genome; but when 4B288 formed the background there was no dose effect exerted on the resistance levels. On the basis of these data, it is suggested that the two *timopheevi* accessions may possess different resistance genes and that the rye genome reacts differently in combination with these genes.

To obtain an ergot resistant triticale, it will be necessary to find a type of resistance that can be expressed in a wheat-rye genetic background. The fact that the best known ergot resistance in wheat is suppressed in the presence of the rye genome has serious implications for triticale breeders. Further studies will be needed to elucidate the genetic mechanism responsible for this behavior.

MANUSCRIPT II

A study of ergot (*Claviceps purpurea* [Fr.] Tul.) susceptibility in *Triticum timopheevi* x *Secale cereale* and *Triticum timopheevi* x *Triticum durum* hybrids.

ABSTRACT

Five accessions of *T. timopheevi* Zhuk. were mated to two *T. durum* and to two *S. cereale* accessions for the purpose of estimating combining abilities for the inheritance of ergot (*C. purpurea* [Fr.] Tul.) susceptibility. Sclerotial frequency, average sclerotium weight, and total sclerotia weight were used to evaluate the susceptibility of the hybrids to two ergot isolates (designated R3A and M15A).

The results indicated that there were significant specific combining ability effects in *T. timopheevi* x *S. cereale* crosses for sclerotial weight for the R3A isolate. When the M15A isolate was considered, there were general and specific combining ability effects in *T. timopheevi* x *T. durum* hybrids for sclerotial frequency and total sclerotia weight. General combining ability effects for sclerotial frequency and total sclerotia weight were found at the 5% level when R3A conidia were used for inoculating the florets of the wheat x wheat plants.

The paired-t-test, t-test, and Tukey's ω-procedure (honestly significant difference procedure) were used to determine the effects of the isolate, male parents, and female parents, respectively. The paired-t-test indicated that the M15A and R3A isolates parasitized the hybrids of the various crosses differentially while the t-tests provided

evidence that each rye and durum male parent must be crossed with a particular female accession to produce the least susceptible plants. Tukey's ω-procedure indicated that the 4B288 *T. timopheevi* accession was the best accession for crossing to line 127 rye and Carleton durum as it conditioned low susceptibility. It was, therefore, recommended for use in further studies.

INTRODUCTION

The best source of ergot (*C. purpurea* [Fr.] Tul.) resistance occurs in *T. timopheevi* Zhuk. (Bernier, 1976). However, this resistance cannot be incorporated into triticale (X *Triticosecale* Wittmack) for immediate use as it does not fully express itself in a *S. cereale* L. background (page 24 of this thesis). Breeders must, therefore, devise an alternative method whereby ergot resistance can be introduced into triticale and consequently a better understanding is needed of the host-parasite interaction of *C. purpurea*, *T. timopheevi*, and *S. cereale*.

Studies conducted on the nature and genetic inheritance of this host-parasite interaction are restricted to F_1 hybrids because the plants are sterile and no advanced generations can be obtained without doubling. Plant characters are needed which quantify the ergot infection in an easily identifiable manner that has practical application in a breeding program. One such character is sclerotial frequency as utilized by Ratanopas (1973) in estimating the degree of ergot resistance. Accordingly, he determined the number of sclerotia as produced in a given number of inoculated florets.

The sole use of sclerotial frequency as the measure of ergot resistance will not identify resistance against fungal aggressiveness (resistance against the fungus once it has established itself in the host). This type of resistance may be useful in triticale breeding programs.

Loveless and Peach (1974) have established that the size of the sclerotium is governed by the host rather than the fungus, hence, a measure of sclerotium size could reflect fungal aggressiveness. One character which conveniently measures sclerotium size is the average weight of sclerotia from a given number of florets harvested at a specified time following inoculation (hereafter designated average sclerotium weight). In order to study this character genetically, a quantitative approach is necessary since fungal aggressiveness is expected to be quantitative in nature (Burnett, 1975).

Another character which can be used as a measure of ergot resistance is the total weight of all the sclerotia of equal maturity produced on a head from a given number of florets harvested at a specified time following inoculation (hereafter designated total sclerotia weight). This character is similar to the Disease Index developed by Ratanopas (1973), in that it combines the criteria of sclerotial number and size. Furthermore, total sclerotia weight has the advantage of being a measurement rather than a rating.

The present study was conducted on *T. timopheevi* x *S. cereale* and *T. timopheevi* x *T. durum* hybrids to determine (1) the efficacy of using sclerotial frequency, average sclerotium weight, and total sclerotia weight as measures of ergot resistance, (2) the effect of using two different *C. purpurea* isolates for inoculation, (3) the general and specific combining ability effects for sclerotial frequency, average sclerotium weight and total sclerotia weight, and (4) the contribution made by each of the male and female parents to the resistance levels of the hybrids.

MATERIALS AND METHODS

T. timopheevi x *T. durum* and *T. timopheevi* x *S. cereale* crosses were made by mating five ergot resistant *timopheevi* accessions (4B286, 4B287, 4B288, 4B289, and 4B573) to two rye accessions (UC 90 and line 127) and to two durum accessions (Stewart and Carleton). The Stewart durum and the UC 90 rye were chosen as completely susceptible wheat and rye parents, respectively, while the Carleton durum and line 127 rye were chosen as less susceptible parents, respectively (Bernier, 1976). All the crosses were embryo cultured according to the method described by Taira and Larter (1978), and were grown in a completely randomized design in a growth room at a constant day/night temperature of 25^{o}C and a minimum light intensity of 7532 lx.

An attempt was made to test 15 plants per cross, but the actual number of plants tested varied due to the loss of some plants during the vegetative stage (Tables 5, 6, 7, and 8). Each surviving plant was tested with *C. purpurea* by the method described by Platford and Bernier (1976). Accordingly, 10 florets on each of three random tillers were inoculated approximately two days before anthesis with either of two single spore isolates. A conidial suspension of each isolate diluted to 10^4 conidiospores per ml was injected into florets using a hypodermic needle. The isolates used were University of Manitoba R3A and M15A.

The R3A isolate was chosen because it was known to be virulent

TABLE 5. The number of *T. timopheevi* x *S. cereale* plants used to determine sclerotial frequency when inoculated with the R3A and M15A isolates

T. timopheevi isolate	*S. cereale* UC 90	*S. cereale* Line 127
	R3A	
4B286	14	16
4B287	12	13
4B288	12	13
4B289	14	14
4B573	10	13
	M15A	
4B286	14	16
4B287	12	13
4B288	12	14
4B289	14	15
4B573	10	13

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TABLE 6. The number of *T. timopheevi* x *T. durum* plants used to determine sclerotial frequency when inoculated with the R3A and M15A isolates

T. timopheevi	*T. durum*	
	Stewart	Carleton
	isolate	
	R3A	
4B286	15	13
4B287	15	15
4B288	15	16
4B289	17	14
4B573	15	15
	M15A	
4B286	14	15
4B287	16	15
4B288	15	16
4B289	15	14
4B573	15	15

TABLE 7. The number of *T. timopheevi* x *S. cereale* plants used to determine average sclerotium weight when inoculated with the R3A and M15A isolates

T. timopheevi	*S. cereale*	
	UC 90	Line 127
	isolate	
	R3A	
4B286	13	16
4B287	12	13
4B288	10	10
4B289	10	14
4B573	10	13
	M15A	
4B286	14	16
4B287	12	13
4B288	11	14
4B289	13	15
4B573	10	13

TABLE 8. The number of *T. timopheevi* x *T. durum* plants used to determine average sclerotium weight when inoculated with the R3A and M15A isolates

T. timopheevi	*T. durum*	
	Stewart	Carleton
	isolate	
	R3A	
4B286	11	13
4B287	15	14
4B288	14	13
4B289	15	12
4B573	14	12
	M15A	
4B286	14	15
4B287	16	12
4B288	15	10
4B289	14	12
4B573	15	15

on the rye and durum accessions but not the five *timopheevi*. The M15A isolate was chosen since its pathogenicity was similar to that of R3A except it was differentially virulent on the 4B286 and 4B289 *timopheevi* accessions (i.e., it could attack 4B286 but not 4B289).

Twenty-five days after inoculation, inoculated heads were harvested and indexed according to the method developed by Ratanopas (Table 9). In addition, sclerotial frequency and total sclerotia weight (weighed in mg) were recorded for each of the heads inoculated with the isolates. From these values the average sclerotium weight per plant and percentage of florets infected were determined. An arc sine transformation was used to transform the percentage data. Because it was necessary to use the arc sine transformation for the genetic analysis, all the data of sclerotial frequency were reported on the transformed scale in order to render the results directly comparable.

The Disease Index developed by Ratanopas (hereafter designated as RDI) was determined for each plant, thus establishing a standard measure of ergot susceptibility. The sensitivity of sclerotial frequency, average sclerotium weight, and total sclerotia weight were then compared to this standard by the use of linear regression. By using the three characters as the dependent variable, RDI as the independent variable, and determining a slope for each of the relationships involved, a value was obtained which equated the change (sensitivity) in each character to the change (sensitivity) in the Disease Index.

A paired-t-test was used to determine if a differential reaction

TABLE 9. Disease reaction caused by *Claviceps purpurea* (Ratanopas, 1973)

Disease reaction	Infection			
	Disease index	Sclerotia† size	Frequency of sclerotia	Honeydew ε
Immune (I)	0	No infection; seed in all florets.	-	1
Very resistant (VR)	1	Abortive reaction (AR) mainly; no sclerotia.	-	1
Resistant (R)	2	AR and sclerotia of size 1 & 2 only.	Not greater than 40%.	1-2
Moderately resistant (MR)	3	Sclerotia mainly size 1 & 2; 1 to 3 sclerotia of size 3.	Not greater than 60%.	1-2
Moderately susceptible (MS)	4	Sclerotia of size 2 & 3.	Not greater than 80%.	3
Susceptible (S)	5	Sclerotia mainly size 3.	Greater than 80%.	4

†1. represents sclerotia smaller than a normal triticale kernel
2. represents sclerotia the same size as a normal triticale kernel
3. represents sclerotia larger than a normal kernel

ε1. no visible honeydew
2. honeydew confined within the glumes
3. honeydew exuding from the florets in small drops
4. honeydew exuding from the florets in large drops and running down the head

occurred between the two isolates depending upon the cross involved. The paired-t-analysis was considered a valid test for the three characters under study as plants were inoculated with each of the two isolates. In order to determine the presence and size of possible bias resulting from a tiller effect (e.g., the isolate used on the first tiller could have an effect on disease reactions expressed in subsequent tillers), a head index was calculated and regressed on sclerotial frequency, average sclerotium weight and total sclerotia weight obtained from the same plant. The head index for each plant was calculated by the following formula:

$$HI = \frac{\sum_{i=1}^{3} T_i}{N}$$

where HI = Head Index

T = Tiller number or position (1 to 6)

N = Number of tillers on the particular plant inoculated with the particular isolate in question.

The data recorded for sclerotial frequency, average sclerotium weight, and total sclerotia weight were analyzed for combining abilities using the model:

$$Y_{mfk} = \mu + \alpha_m + \beta_f + (\alpha\beta)_{mf} + e_{mfk}$$ (Baker, 1978; Friars, 1978)

where Y_{mfk} = the plant observation of the k_{th} full sib of the m_{th} paternal plant crossed to the f_{th} maternal plant

μ = overall mean

α_m = fixed effect of the m_{th} paternal plant

β_f = fixed effect of the f_{th} maternal plant

$(\alpha\beta)_{mf}$ = interaction between the m_{th} paternal and f_{th} maternal plant

e_{mfk} = overall random variation

In this analysis, all effects were considered to be fixed.

The mean squares for male and female parents were considered independent estimates of general combining ability (g.c.a.), while the mean square of the male x female interaction was considered an estimate of specific combining ability (s.c.a.) (Friars, 1978; Baker, 1978).

In order to detect the male(s) and female(s) which produced the most resistant cross(es) the data had to be handled in the following manner. To determine the better males, the mean sclerotial frequency, average sclerotium weight, and total sclerotia weight for the two ryes or the two durums mated to the same female accessions were compared using a t-test. To determine the superior females, Tukey's ω-procedure (honestly significant difference procedure; Steel and Torrie, 1960) was employed subsequent to the following analyses. One way anova were performed on the data of the five *timopheevi* wheats crossed to the same male, and the error mean squares obtained in these tables were used in Tukey's ω-procedure. The mean sclerotial frequency, average sclerotium weight, and total sclerotia weight for the five *timopheevi* crosses to each male were tested individually, thus eliminating the interaction arising from the male which was excluded from the analysis.

RESULTS

Sensitivity

All but two of the regressions between the Disease Index (RDI) and the parameters sclerotial frequency, average sclerotium weight, and total sclerotia weight were found to be highly significant. The two exceptions involved the R3A isolate inoculated into *T. timopheevi* x *T. durum* florets (Table 10). The highly significant regressions between the data indicate that a strong relationship exists between the three characters studied and the Disease Index. In the significant regressions, all the slopes were positive and sclerotial frequency, average sclerotium weight, and total sclerotia weight were compared on an approximate scale of 10 to 20 units, 5 to 8 units, and 20 to 100 units for each single unit of Disease Index, respectively. The number of units observed for each parameter was considered its sensitivity.

Isolate Effect

In order that the M15A and the R3A isolates could be compared using the paired-t-test, a determination was made of the tiller effect on sclerotial frequency, on average sclerotium weight, and on total sclerotia weight. Only one of the regressions obtained for average sclerotium weight and total sclerotia weight were significant (Table 11). These significances involved hybrids

TABLE 10. Slopes and significance of the regression lines of sclerotial frequency, average sclerotium weight, and total sclerotia weight on Disease Index

Cross		Slopes and significances					
		Sclerotial[Σ] frequency		Average sclerotium[+] weight		Total sclerotia weight	
		M15A	R3A	M15A	R3A	M15A	R3A
T. timopheevi x *S. cereale*	(line 127)	10.26**	8.66**	7.44**	7.74**	84.26**	94.54**
T. timopheevi x *S. cereale*	(UC 90)	16.18**	15.79**	5.24**	5.26**	79.15**	52.48**
T. timopheevi x *T. durum*	(Carleton)	11.21**	9.35**	7.03**	-0.61ns	19.92**	55.20**
T. timopheevi x *T. durum*	(Stewart)	9.68**	18.18**	6.38**	-0.08ns	68.00**	23.91**

Σ % transformed

+ mg

** significant at the 1% level

ns not significant at the 5% level

TABLE 11. Slopes and significance of the regression lines of sclerotial frequency, average sclerotium weight and total sclerotia weight on Head Index

timopheevi parent	Male parent	Slopes and significances					
		Sclerotial frequency		Average sclerotium weight		Total sclerotia weight	
		R3A	M15A	R3A	M15A	R3A	M15A
4B573	UC 90	0.03^{ns}	-0.13^{ns}	1.61^{ns}	-6.96^{ns}	33.88^{ns}	-66.76^{ns}
	127	0.13^{ns}	-0.04^{ns}	17.91^{ns}	-7.18^{ns}	34.94^{ns}	-50.94^{ns}
4B286	UC 90	-0.05^{ns}	-0.13^{ns}	0.28^{ns}	-2.64^{ns}	0.61^{ns}	-31.22^{ns}
	127	-0.14^{ns}	-0.03^{ns}	-2.67^{ns}	7.89^{ns}	-49.96^{ns}	63.68^{ns}
4B287	UC 90	0.09^{ns}	0.08^{ns}	-0.10^{ns}	-5.01^{ns}	11.84^{ns}	0.90^{ns}
	127	-0.06^{ns}	0.02^{ns}	-1.29^{ns}	-5.80^{ns}	-13.74^{ns}	-18.38^{ns}
4B288	UC 90	-0.11^{ns}	0.5^{ns}	-3.14^{ns}	14.57^{*}	-12.74^{ns}	77.14^{ns}
	127	0.08^{ns}	-0.04^{ns}	0.91^{ns}	-3.81^{ns}	7.28^{*}	-26.37^{ns}
4B289	UC 90	0.01^{ns}	-0.09^{ns}	1.60^{ns}	-11.09^{ns}	-3.84^{ns}	-40.17^{ns}
	127	-0.05^{ns}	-0.07^{ns}	-1.48^{ns}	-1.26^{ns}	-9.65^{ns}	-6.11^{ns}
4B573	Stewart	0.05^{ns}	-0.03^{ns}	2.86^{ns}	-1.65^{ns}	1.12^{ns}	-11.52^{ns}
	Carleton	0.06^{ns}	-0.02^{ns}	-0.06^{ns}	-2.07^{ns}	2.66^{ns}	-7.56^{ns}
4B286	Stewart	0.04^{ns}	0.01^{ns}	1.84^{ns}	-2.16^{ns}	10.64^{ns}	-191.61^{ns}
	Carleton	0.04^{ns}	-0.12^{ns}	-1.18^{ns}	-1.59^{ns}	-0.41^{ns}	-19.52^{ns}
4B287	Stewart	0.04^{ns}	-0.07^{ns}	-1.76^{ns}	-6.46^{ns}	2.79^{ns}	-40.05^{ns}
	Carleton	-0.04^{ns}	-0.05^{ns}	1.39^{ns}	-3.54^{ns}	-0.35^{ns}	-15.25^{ns}
4B288	Stewart	0.01^{ns}	-0.10^{ns}	0.53^{ns}	2.55^{ns}	2.70^{ns}	-10.89^{ns}
	Carleton	-0.02^{ns}	-0.13^{ns}	0.47^{ns}	-1.27^{ns}	2.06^{ns}	-13.38^{ns}
4B289	Stewart	-0.05^{ns}	-0.03^{ns}	0.29^{ns}	-2.05^{ns}	-1.53^{ns}	-14.34^{ns}
	Carleton	-0.01^{ns}	0.00^{ns}	0.49^{ns}	1.33^{ns}	0.58^{ns}	8.56^{ns}

^{ns} not significant

* significant at the 5% level

with 4B288 as the female parent. The absence of signicance in the data of the remaining crosses indicated that the tiller effect was removed by randomization. Consequently, it was possible to make comparisons between the isolates.

The paired-t-tests indicated the differences between the R3A and M15A isolates were significant for sclerotial frequency, average sclerotium weight, and total sclerotia weight obtained from various F_1 of *T. timopheevi* x *S. cereale* and *T. timopheevi* x *T. durum* crosses (Tables 12 and 13). Fewer significant differences were found between the isolates in the *T. timopheevi* x *S. cereale* data (Table 12) than in the *T. timopheevi* x *T. durum* data (Table 13). The mean sclerotial frequencies and average sclerotia weights of the M15A isolate were consistently larger than those of the R3A isolate (Figures 1 and 2). The host had a tendency to be highly susceptible to both sources of inoculum when non-significance occurred between isolates, e.g., sclerotial frequency expressed in the data of the 4B573 x UC 90 and 4B287 x 90 crosses (Figure 1).

Combining Ability Analysis

There was evidence of significant combining ability effects in all the data except for total sclerotia weight and average sclerotium weight of the wheat x rye and wheat x wheat F_1 inoculated with R3A conidia. Also, no significance was found for sclerotial frequency, average sclerotium weight, and total sclerotium weight of wheat x rye F_1 inoculated with M15A conidia. Significant specific combining

TABLE 12. Disease Index, significant paired-t-test differences, and means between isolates for the characters, sclerotial frequency, average sclerotium weight, and total sclerotia weight of *T. timopheevi* x *S. cereale* crosses

timopheevi parent	Rye parent	means with paired-t-test significances										
		Disease Index		Sclerotial frequency*			Average sclerotium weight			Total sclerotia weight		
		R3A	M15A	R3A	M15A	Sig	R3A	M15A	Sig	R3A	M15A	Sig
4B573	UC 90	3.52	3.45	43.6	48.9	ns	18.4	25.8	ns	117.3	170.9	ns
4B286	UC 90	2.51	2.95	29.5	40.3	.01	8.7	16.1	.01	24.4	108.0	.01
4B287	UC 90	2.93	3.16	41.7	43.8	ns	17.6	24.4	.01	102.8	121.3	ns
4B288	UC 90	2.63	3.06	35.2	40.6	ns	16.4	22.5	ns	88.8	128.4	.05
4B289	UC 90	2.84	3.11	27.0	44.7	.01	19.5	29.3	ns	74.7	185.1	.01
4B573	127	2.87	3.56	34.1	49.3	.01	17.3	27.0	.01	81.4	174.7	.01
4B286	127	3.06	3.67	42.1	52.9	ns	16.7	31.8	.01	93.5	216.0	.01
4B287	127	2.57	2.81	24.9	32.3	ns	9.5	21.6	.01	35.1	114.3	ns
4B288	127	1.90	2.92	16.0	42.6	.01	9.3	27.9	.05	15.5	124.7	.01
4B289	127	2.28	3.23	29.8	47.4	.01	9.1	25.3	.01	37.7	140.9	.01

* arc sine transformed means

ns not significant at the 5% level

.05 significant at the 5% level

.01 significant at the 1% level

TABLE 13. Disease Index, significant paired-t-test differences, and means between isolates for the characters, sclerotial frequency, average sclerotium weight, and total sclerotia weight of *T. timopheevi* x *T. durum* crosses

timopheevi parent	Durum parent	means with paired-t-test significances										
		Disease Index		Sclerotial frequency*			Average sclerotium weight			Total sclerotia weight		
		R3A	M15A	R3A	M15A	Sig	R3A	M15A	Sig	R3A	M15A	Sig
4B573	Stewart	2.20	2.58	24.1	34.7	.05	9.77	20.9	.01	29.8	86.9	.01
4B286	Stewart	2.12	2.45	19.6	33.1	.01	10.9	18.3	.01	24.0	64.3	.01
4B287	Stewart	2.14	2.48	22.0	28.2	.05	8.5	23.3	.01	17.9	80.8	.01
4B288	Stewart	2.04	2.75	19.7	34.0	.01	8.8	23.1	.01	20.5	90.8	.01
4B289	Stewart	2.04	2.60	19.2	27.5	.01	7.9	22.0	.01	27.5	82.6	.01
4B573	Carleton	1.92	2.17	12.5	20.0	.01	8.3	17.0	.05	12.4	24.5	.01
4B286	Carleton	2.61	2.46	29.1	33.0	ns	8.9	20.0	.01	29.5	84.1	.01
4B287	Carleton	2.07	2.39	17.8	24.0	.05	8.5	18.7	.01	15.2	53.7	.01
4B288	Carleton	2.03	2.08	14.2	15.9	ns	7.4	14.9	.01	12.9	39.2	.01
4B289	Carleton	2.04	2.21	13.5	21.3	.05	7.7	14.2	.01	13.3	42.9	.01

* arc sine transformed means

ns not significant at the 5% level

.05 significant at the 5% level

.01 significant at the 1% level

Figure 1. Bar graphs illustrating the susceptibility (sclerotial frequency) levels of hybrids inoculated with the R3A and M15A isolates.

573 indicates 4B573

286 indicates 4B286

287 indicates 4B287

288 indicates 4B288

289 indicates 4B289

127 indicates line 127

Carl indicates Carleton

Ste indicates Stewart

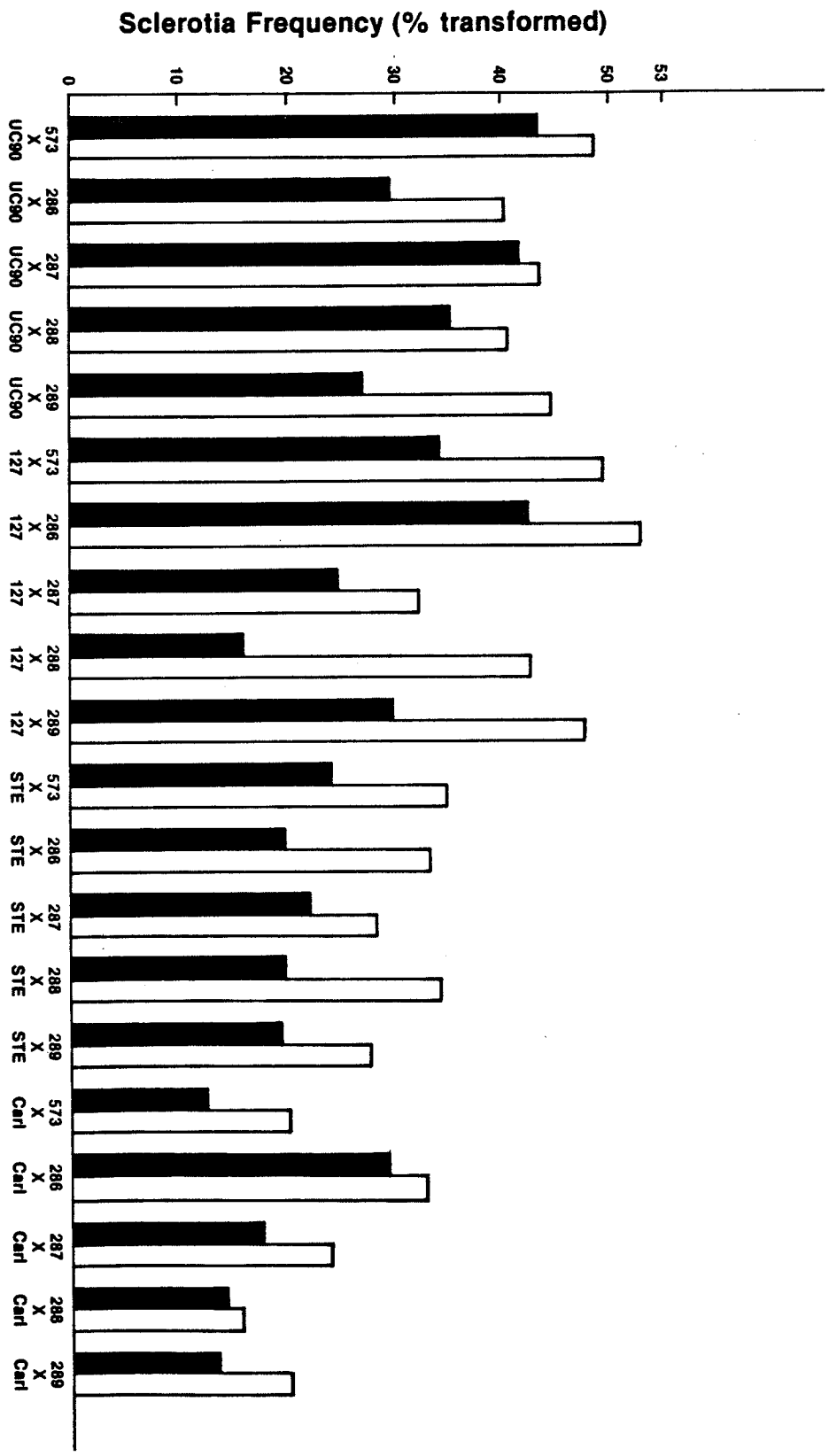
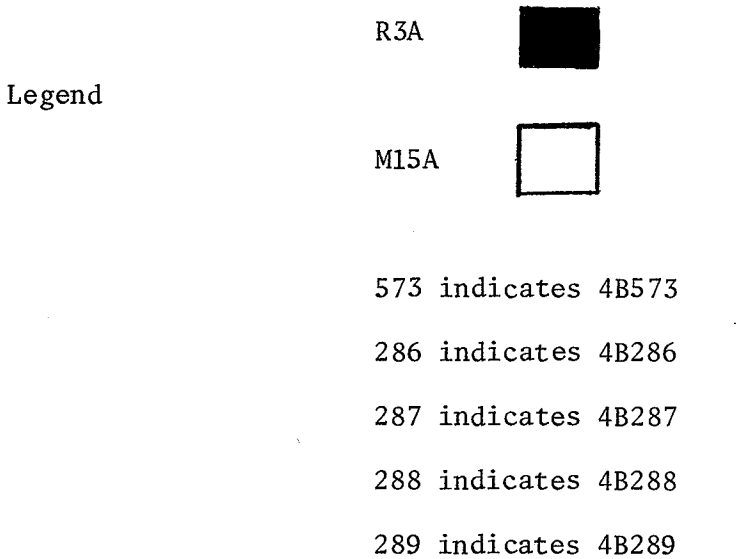
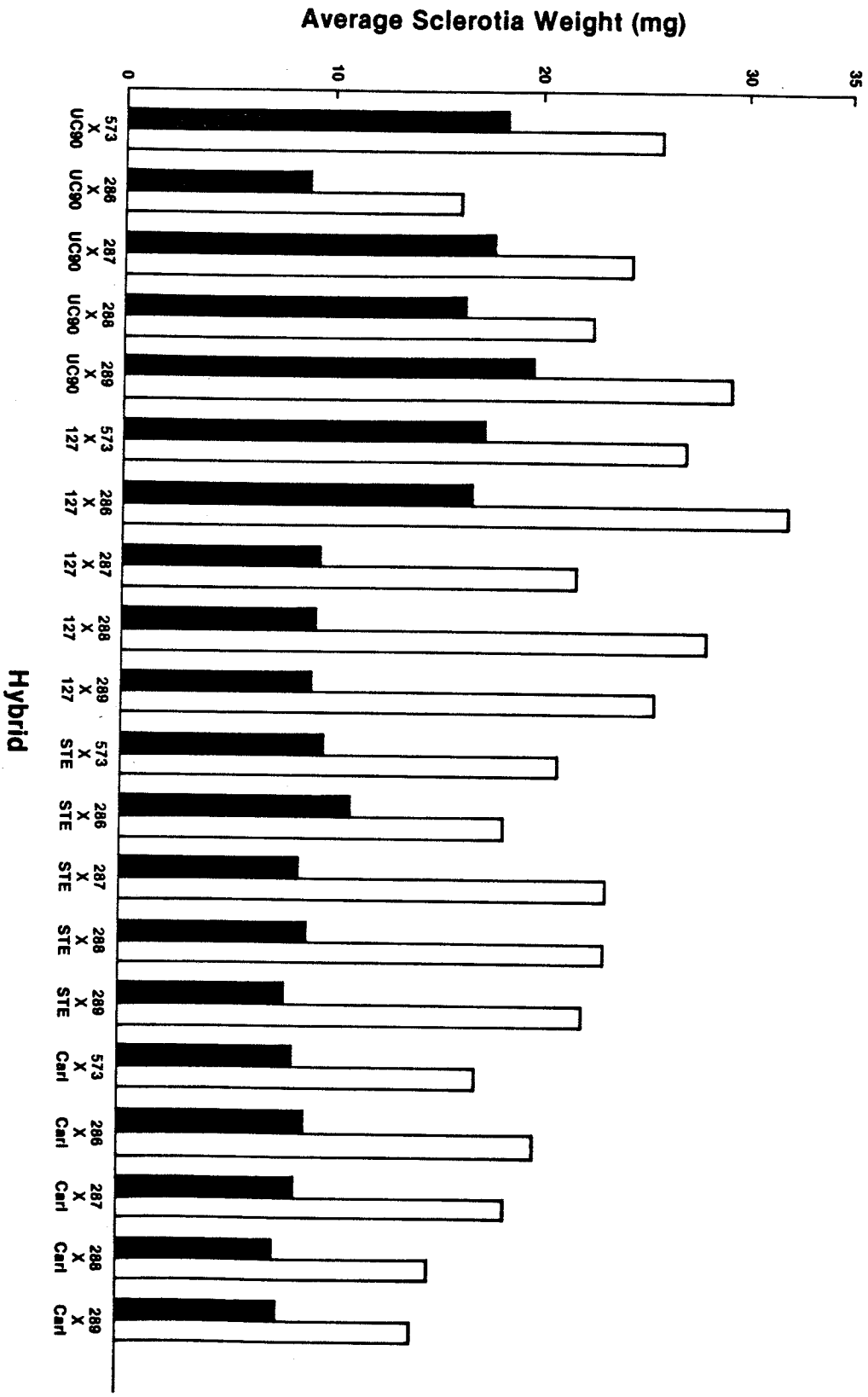

Sclerotia Frequency (% transformed)
0
10
20
30
40
50
53
Hybrid
573 X UC90
286 X UC90
287 X UC90
288 X UC90
289 X UC90
573 X 127
286 X 127
287 X 127
288 X 127
289 X 127
573 X STE
286 X STE
287 X STE
288 X STE
289 X STE
573 X Carl
286 X Carl
287 X Carl
288 X Carl
289 X Carl

Figure 2. Bar graphs illustrating the susceptibility (average sclerotium weight) levels of hybrids inoculated with the R3A and M15A isolates.




Average Sclerotia Weight (mg)
0
10
20
30
35
Hybrid
573 X UC90
286 X UC90
287 X UC90
288 X UC90
289 X UC90
573 X 127
286 X 127
287 X 127
288 X 127
289 X 127
573 X STE
286 X STE
287 X STE
288 X STE
289 X STE
573 X Carl
286 X Carl
287 X Carl
288 X Carl
289 X Carl

ability effects occurred for sclerotial frequency and average sclerotium weight when *T. timopheevi* x *S. cereale* hybrids were inoculated with the R3A isolate (Table 14). Similarly, significant general combining ability effects were obtained for sclerotial frequency and total sclerotia weight when *T. timopheevi* x *T. durum* hybrids were inoculated with the same isolate (Table 15). Both general and specific combining ability effects were observed for sclerotial frequency and total sclerotia weight in the instances where *T. timopheevi* x *T. durum* plants were inoculated with the M15A isolate.

Male Effect

Significant differences occurred in the susceptibility levels of the hybrids when both *S. cereale* and *T. durum* were used as pollen parents and crossed to various *T. timopheevi* accessions (Tables 16 and 17). The UC 90 and line 127 ryes altered sclerotial frequency of hybrids involving 4B287 and 4B288 and total sclerotia weight of hybrids involving 4B286, 4B287, and 4B288 when the R3A isolate was used for inoculations (Table 16). Only average sclerotium weight and total sclerotia weight of hybrids involving 4B286 exhibited a rye effect when the M15A isolate was used for inoculations (Table 16). In contrast to this, the F_1 progeny with Carleton and Stewart durums as the paternal parents expressed a greater number of significant differences in the data of the M15A isolate. Total sclerotia weight for hybrids with 4B573 as the maternal parent was

TABLE 14. Mean squares from combining ability analyses of variance for sclerotial frequency and average sclerotium weight for *T. timopheevi* x *S. cereale* crosses inoculated with the R3A isolate

	g.c.a. (females)		g.c.a. (males)		s.c.a. (male x female)		error	
Character	df	ms	df	ms	df	ms	df	ms
Sclerotial freq.	4	736.31	1	598.92	4	1,204.73*	118	353.54
Average scl. wt.	4	106.74	1	268.37	4	309.33*	111	91.23

*indicates significance at the 5% level.

Table 15. Mean squares from combining ability analyses of variance for sclerotial frequency, average sclerotium weight, and total sclerotia weight for *T. timopheevi* x *T. durum* crosses inoculated with the M15A and R3A isolates

Character	Isolate	g.c.a. (females)		g.c.a. (males)		s.c.a. (mxf)		Error	
		df	ms	df	ms	df	ms	df	ms
Sclerotial freq.	R3A	4	634.40**	1	470.10*	4	78.05	140	114.18
Total scl. wt.	R3A	4	690.93*	1	578.43°	4	477.41°	123	209.55
Sclerotial freq.	M15A	4	393.75°	1	2,695.80**	4	459.94*	140	169.90
Avg. scl. wt.	M15A	4	42.86	1	992.82**	4	108.65	128	60.66
Total scl. wt.	M15A	4	18,314.35**	1	31,675.23**	4	54,214.38**	128	186.75

*, **, and ° indicate the 5%, 1%, and 10% levels, respectively

TABLE 16. The t-test significance levels for means of sclerotial frequency, average sclerotium weight, and total sclerotia weight for *T. timopheevi* x *S. cereale* crosses inoculated with two isolates of *C. purpurea*

timopheevi parent	Rye parent	means with t-test significances											
		Sclerotial frequency*				Average sclerotium weight				Total sclerotia weight			
		R3A	Sig	M15A	Sig	R3A	Sig	M15A	Sig	R3A	Sig	M15A	Sig
573	UC 90	43.6	ns	48.9	ns	18.4	ns	25.8	ns	117.3	ns	170.9	ns
	127	34.1		49.3		17.3		27.0		81.4		174.7	
286	UC 90	29.5	ns	40.3	ns	8.7	ns	16.1	.01	24.4	.05	108.1	.01
	127	42.1		52.9		16.7		31.8		93.5		216.0	
287	UC 90	41.7	.01	43.8	ns	17.6	ns	24.4	ns	102.8	.01	121.3	ns
	127	24.9		32.3		9.5		21.6		35.2		114.3	
288	UC 90	35.2	.05	40.6	ns	16.4	ns	22.5	ns	88.8	.05	128.4	ns
	127	16.0		42.5		9.3		27.9		15.5		124.7	
289	UC 90	27.0	ns	44.7	ns	19.5	ns	29.3	ns	74.7	ns	185.1	ns
	127	29.8		47.4		9.1		25.3		37.7		140.9	

* arc sine transformed means

ns not significant at the 5% level

.05 significant at the 5% level

.01 significant at the 1% level

TABLE 17. The t-test significance levels for means of sclerotial frequency, average sclerotium weight, and total sclerotia weight for *T. timopheevi* x *T. durum* crosses inoculated with two isolates of *C. purpurea*

timopheevi parent	Durum parent	means with t-test significances											
		Sclerotial frequency*				Average sclerotium weight				Total sclerotia weight			
		R3A	Sig	M15A	Sig	R3A	Sig	M15A	Sig	R3A	Sig	M15A	Sig
573	Stewart	24.1	ns	34.7	.01	9.77	ns	20.9	ns	29.8	.05	86.9	.01
	Carleton	12.5		20.0		8.30		17.0		12.4		24.5	
286	Stewart	19.6	ns	33.1	ns	10.9	ns	18.3	ns	24.0	ns	64.3	ns
	Carleton	29.1		33.0		8.9		20.0		29.5		84.1	
287	Stewart	22.0	ns	28.3	ns	8.5	ns	23.3	ns	17.9	ns	80.8	ns
	Carleton	17.8		24.0		8.5		18.7		15.2		53.7	
288	Stewart	19.7	ns	34.0	.01	8.8	ns	23.1	.05	20.5	ns	90.8	.05
	Carleton	14.2		15.9		7.4		14.9		12.9		39.2	
289	Stewart	19.2	ns	27.5	ns	7.9	ns	22.0	.05	27.5	ns	82.6	.05
	Carleton	13.5		21.3		7.7		14.2		13.3		42.9	

* arc sine transformed means

ns not significant at the 5% level

.05 significant at the 5% level

.01 significant at the 1% level

significantly different in the R3A isolate data, while sclerotial frequency for hybrids with the 4B573 and 4B288 maternal parents, average sclerotium weight for hybrids with the 4B288 and 4B289 maternal parents, and total sclerotia weight for the hybrids with the 4B573, 4B288 and 4B289 maternal parents were significantly different in the M15A isolate data.

Female Effect

Tukey's ω-procedure was used to determine the susceptibility relationships of the five *timopheevi* accessions mated to the same rye or durum. In order to simplify the tables, means which can be found in Tables 12 and 13 were omitted and only similar subsets are presented. The "a" and "d" indicate the most and least resistant subsets, respectively, not found to be significantly different (Tables 18 to 21). Hybrids expressed few differences in susceptibility levels when the *timopheevi* accessions were mated to the UC 90 rye, but were differentiated into subsets when mated to the line 127 rye (Tables 18 and 19). Consequently, the *timopheevi* accessions were not maintaining the same resistance levels when crossed to different ryes. Also noticeable in the data were 4B286 hybrids which ranked similar to other hybrids when mated to UC 90 rye, but which ranked in different subsets when mated to the line 127 rye (Tables 18 and 19). Few significant differences occurred when hybrids involved Stewart durum (Tables 20 and 21). Considering total sclerotia weight, the 4B286 conditioned the most resistant hybrid in the M15A isolate data (Table 21), while all but 4B573 hybrids were in the most

TABLE 18. Significant subsets as identified by Tukey's ŵ-procedure of sclerotial frequency, average sclerotium weight, and total sclerotia weight for *T. timopheevi* x *S. cereale* hybrids inoculated with the R3A isolate of *C. purpurea*

UC 90 rye		127 rye	
timopheevi parent†	Subsetε	*timopheevi* parent†	Subsetε
Character			
sclerotial frequency			
4B289	a	4B288	a
4B286	a	4B287	ab
4B288	a	4B289	ab
4B287	a	4B573	ab
4B573	a	4B286	b
average sclerotium weight			
4B286	a	4B289	a
4B288	b	4B288	a
4B287	b	4B287	a
4B573	b	4B286	a
4B289	b	4B573	a
total sclerotia weight			
4B286	a	4B288	a
4B289	a	4B289	a
4B288	a	4B287	a
4B287	a	4B573	b
4B573	a	4B286	c

†the wheat parents are listed by mean size with the smallest mean at the top of the list

ε*timopheevi* accessions followed by the same letter are not significantly different as tested by Tukey's ω-procedure; "a" designates the most resistant subset, "c" the least resistant subset.

TABLE 19. Significant subsets as identified by Tukey's ω-procedure of sclerotial frequency, average sclerotium weight, and total sclerotia weight for *T. timopheevi* x *S. cereale* hybrids inoculated with the M15A isolate of *C. purpurea*

UC 90 rye		127 rye	
timopheevi parent†	Subset$^{\varepsilon}$	*timopheevi* parent†	Subset$^{\varepsilon}$
Character			
sclerotial frequency			
4B286	a	4B287	a
4B288	a	4B288	ab
4B287	a	4B289	ab
4B289	a	4B573	ab
4B573	a	4B286	b
average sclerotium weight			
4B286	a	4B287	a
4B288	a	4B289	a
4B287	a	4B573	a
4B573	a	4B288	a
4B289	a	4B286	a
total sclerotia weight			
4B286	a	4B287	a
4B288	a	4B288	a
4B287	a	4B289	a
4B573	a	4B573	a
4B289	a	4B286	a

† the wheat parents are listed by mean size with the smallest mean at the top of the list

$^{\varepsilon}$ *timopheevi* accessions followed by the same letter are not significantly different as tested by Tukey's ω-procedure; "a" designates the most resistant subset, "b" the least resistant subset

TABLE 20. Significant subsets as identified by Tukey's ω-procedure of sclerotial frequency, average sclerotium weight, and total sclerotia weight for *T. timopheevi* x *T. durum* hybrids inoculated with the R3A isolate of *C. purpurea*

Stewart durum		Carleton durum	
timopheevi parent†	Subset$^{\varepsilon}$	*timopheevi* parent†	Subset$^{\varepsilon}$
Character			
sclerotial frequency			
4B289	a	4B573	a
4B286	a	4B289	a
4B288	a	4B288	a
4B287	a	4B287	a
4B573	a	4B286	b
average sclerotium weight			
4B289	a	4B289	a
4B286	a	4B288	a
4B288	a	4B573	a
4B287	a	4B286	a
4B573	a	4B287	a
total sclerotia weight			
4B289	a	4B573	a
4B287	ab	4B288	a
4B288	ab	4B289	a
4B286	ab	4B287	a
4B573	b	4B286	b

† the wheat parents are listed by mean size with the smallest mean at the top of the list

$^{\varepsilon}$ *timopheevi* accessions followed by the same letter are not significantly different as tested by Tukey's ω-procedure; "a" designates the most resistant subset, "b" the least resistant subset.

TABLE 21. Significant subsets as identified by Tukey's ω-procedure of sclerotial frequency, average sclerotium weight, and total sclerotia weight for *T. timopheevi* x *T. durum* hybrids inoculated with the M15A isolate of *C. purpurea*

Stewart durum		Carleton durum	
timopheevi parent†	Subset€	*timopheevi* parent†	Subset€
	sclerotial frequency		
4B289	a	4B288	a
4B287	a	4B573	a
4B286	a	4B289	ab
4B288	a	4B287	ab
4B573	a	4B286	b
	average sclerotium weight		
4B286	a	4B573	a
4B573	a	4B289	a
4B289	a	4B288	a
4B288	a	4B287	a
4B287	a	4B286	a
	total sclerotia weight		
4B286	a	4B573	a
4B287	b	4B288	b
4B289	b	4B289	bc
4B573	b	4B287	c
4B288	b	4B286	d

† the wheat parents are listed by mean size with the smallest mean at the top of the list

€ *timopheevi* accessions followed by the same letter are not significantly different as tested by Tukey's ω-procedure; "a" designating the most resistant subset, "b" the least resistant subset

resistant subset in the R3A isolate data (Table 20). When crossed to Carleton, the 4B286 accession conditioned the more susceptible hybrids inoculated with M15A and R3A isolates.

DISCUSSION

Significance should occur between closely related variables. Ratanopas' Disease Index (RDI) is related to sclerotial frequency, average sclerotium weight, and total sclerotia weight in the following manner: (1) sclerotial frequency is a component of RDI, (2) the rating of sclerotial size in RDI should vary directly with average sclerotium weight, i.e., larger sclerotia are expected to weigh more than smaller sclerotia, and (3) classification of resistance based on both RDI and total sclerotia weight include a combination of sclerotial frequency and sclerotium weight. Because of these relationships, it was unexpected to obtain two regressions which were not significant (Table 11). One possible explanation for the loss of significance is the chance deviations of values from the expected. It is noteworthy, however, that both exceptions involved the parameter "average sclerotium weight" in the *T. timopheevi* x *T. durum* crosses inoculated with the R3A isolate.

Because the remaining regressions were significant, sclerotial frequency, average sclerotium weight, and total sclerotia weight were thought to be useful criteria for measuring ergot resistance. Each of the parameters exhibited adequate ranges within which the plant breeder could select, e.g., sclerotia produced on plants indexed as resistant were equal to or smaller than normal kernels, but still could be divided into five or eight classes when average sclerotium weight

was considered. Sensitivity on this scale allows the breeder to apply adequate selection pressure so that progress can be made in developing polygenic resistance using as the index, average sclerotium weight.

Both frequency of sclerotia and size of sclerotia have been used in previous studies to estimate ergot resistance (Ratanopas, 1973; Platford and Bernier, 1976; Schmidt and Lucken, 1976). In the study conducted by Schmidt and Lucken (loc cit), frequency of sclerotia was found to be the most precise measurement of ergot resistance which is similar to the results found in this study. In previous studies, there is no indication of strict time limits being placed on sclerotial growth; hence, plants which were parasitized for a longer period of time may not have been detected in sclerotial size estimates even though they may have possessed genes which restricted the rate of development. In the present study, a strict time limit was imposed and average sclerotium weight should reflect resistance to fungal aggressiveness. Comparisons, therefore, should not be made with sclerotial size estimates obtained in previous studies.

The merits of any selection character must be considered before it is utilized in a plant breeding program. Of the three characters studied, sclerotial frequency has the most dramatic expression and is simple to ascertain any time after sclerotia are formed. Average sclerotium weight, on the other hand, is the most laborious to determine and is not as striking to the eye of the breeder as is the absence of sclerotia. Total sclerotia weight is intermediate to the

two previous characters in its difficulty of assessment in that weight measurements are necessary at a set time period following inoculation, but no further calculations are needed. The resultant progress achieved in the separate components (that is sclerotial number and weight) will be less in total sclerotia weight than if the components were selected separately. Thus, in order that a character can be effectively integrated into a breeding program, a balance must be obtained between the labour involved and the progress expected. For the most part, sclerotial frequency will be chosen mainly because of its dramatic expression. But, the breeder should not be discouraged at this time from using average sclerotium weight even though there were few significant differences observed (Tables 16 through 21). The present material was selected on the basis of sclerotial frequency and little selection has been carried out on sclerotia size *per se*. If a concentrated effort is made to reduce sclerotial size, the response may well be justifiable.

During the course of this study it became evident that *C. purpurea* parasitized plants of *T. timopheevi* x *S. cereale* and *T. timopheevi* x *T. durum* crosses in a characteristic pattern different to that of the parental accessions. The M15A isolate attacked the 4B286 and 4B289 accessions differentially while hybrids with these accessions as the maternal parents were not attacked differentially (Tables 12 and 13). Rather, pathogenicity on these hybrid hosts was intermediate to that of the maternal and paternal parent.

In the combining ability analyses of *T. timopheevi* x *T. durum*, mean squares for males, and males x females, were not significant at the 5% level for total sclerotia weight in the R3A data (Table 15). A general combining ability effect could have been expected since the male parent was a wheat. The loss of significance of these mean squares may have been masked by the non-significant weight (average sclerotium weight) component. In all likelihood, both general and specific combining ability effects were present as in total sclerotia weight of the M15A isolate data. Support for this was derived by the fact that the mean square for male x female interaction (S.C.A.) was significant at the 10% level. In similar fashion, sclerotial frequency for *T. timopheevi* x *T. durum* crosses inoculated with M15A conidia, were shown to exhibit a general combining ability effect for both the male and the female mean squares at the 10% level (Table 15). Only Stewart and Carleton exhibited a significant general combining ability effect for average sclerotium weight (in the M15A isolate data), indicating that the remainder of the accessions possessed little variability for sclerotial size resistance.

The results of the *T. timopheevi* x *T. durum* crosses compare favourably to those of Schmidt and Lucken (1976). They found general and specific combining ability effects for number and size of sclerotia, however, they attributed most of the variation to a general combining ability effect. In the present study, specific combining ability effects were much more likely to occur since species crosses were investigated, whereas Schmidt and Lucken (loc cit) examined cultivar crosses. Thus, it was not surprising to

find that specific combining ability effects were occurring in the *T. timopheevi* x *T. durum* crosses.

T. timopheevi x *S. cereale* are wider crosses than *T. timopheevi* x *T. durum*. Consequently, one can expect to find specific combining ability effects in these wider crosses; this was the case in the present data (Table 14). The specific combining ability effects present a major problem to the triticale breeder for the following reasons: a general combining ability effect is indicative of an additive type of gene action, whereas a specific combining ability effect is indicative of a dominant and/or epistatic gene action. Because triticale is a self-pollinating species, only additive types of gene action can be fixed. Therefore, in order to breed an ergot resistant triticale, dominant and/or epistatic gene actions must be selected against and fixed.

It was not known if resistance of a wide cross could be altered by replacing the susceptible parent with a more resistant parent. This effect was examined by studying the susceptibility levels conditioned in crosses of *T. timopheevi* to the two durums, Carleton and Stewart. Carleton had previously been shown to be more resistant than Stewart. The difference in resistance levels of these cultivars can be seen in the data of Platford and Bernier (1976) where an equal concentration of conidia of the M1 isolate was used to inoculate both cultivars. In their data, Carleton exhibited a 21% infection frequency while Stewart exhibited a 68% infection frequency. In the present study, R3A was a single spore isolate out of M1, and the virulence of this single spore isolate in this study can be expected

to deviate from those obtained by Platford and Bernier (loc cit). Consequently, the important aspect of these data is the fact that the Carleton crosses produced a consistently lower sclerotial frequency than did the Stewart crosses. Even though this difference is not statistically significant in most comparisons, it is felt that the Carleton has a small but positive effect on the resistance level of *T. timopheevi* x *T. durum* hybrids at the inoculation temperature used. Whether or not this effect would occur at different temperatures cannot be determined from this study, as tests were conducted in only one regime.

An attempt was made to carry out a similar comparison with the ryes. The 127 rye was chosen to be representative of a less susceptible rye than the UC 90 rye. At best, however, the difference in susceptibility of the two ryes was very small. Consequently, it was not surprising to find the infection levels of the *T. timopheevi* x *S. cereale* hybrids involving the line 127 rye were not consistently lower than the infection levels of the crosses involving UC 90.

To be of value as a source of ergot resistance in *T. timopheevi* x *S. cereale* hybrids and eventually in triticale, the *timopheevi* accession must be able to consistently condition low levels of susceptibility in hybrids. As previously pointed out, the 4B286 accession conditioned unstable levels in hybrids to various ryes. Because triticale possesses various ryes in its background, the 4B286 accession was considered a poor choice of resistance at this time (Table 16). The 4B573 accession was eliminated on the basis that it consistently conditioned high levels of susceptibility in hybrids (Tables 18 and 19) and was usually grouped in the most susceptible subset by Tukey's ω-procedure. Also noticeable in most

comparisons of Tukey's multiple range test was the inclusion of the three *timopheevi* accessions, 4B287, 4B288, and 4B289 in the most resistant subset. Of these three accessions, 4B288 is the one which is recommended for use at this time. This is based on the lower susceptibility levels of the 4B288 accession when mated to Carleton and inoculated with the M15A isolate (Tables 17 and 21), also when mated to the line 127 rye and inoculated with the R3A isolate (Tables 16 and 18).

Based on the results of this study, it can be concluded that a major breeding effort will be necessary before an ergot resistant triticale can be obtained. The fact that susceptibility to this pathogen is inherited as a dominant and/or epistatic gene action has serious implications for triticale breeders. Thus, any breeding effort must concentrate on this aspect of the host parasite interaction.

GENERAL DISCUSSION (OVERALL)

A high level of ergot resistance such as the one possessed by *T. timopheevi* is needed in triticale. At present, the full component of resistance in *timopheevi* is not expressed when combined with the rye genome. Consequently, a rye must be developed which will not effect the expression of ergot resistance when it is introduced into a *timopheevi* triticale.

Three parameters thought to have potential as measures of ergot resistance were examined in this study. In order to produce a resistant *timopheevi*, a triticale breeder must select against each of the parameters, (i.e., a high frequency of sclerotia or a high sclerotium weight). This requisite presents a major problem as the parameters are conditioned by a specific combining ability effect. A specific combining ability effect is generally thought to be indicative of the presence of dominance and/or epistatic gene actions and cannot, therefore, be fixed in a self-pollinating species such as triticale.

The present study does not conclusively determine if the susceptibility in the wheat x rye hybrids is conditioned by a dominant or epistatic gene action. However, if susceptibility is conditioned by a dominant gene action, it should be possible to identify recessive genes governing resistance in a *S. cereale* population. To the author's knowledge, no such resistance has been found in the rye

populations investigated to date. This could signify that the susceptibility of the wheat x rye hybrids is affected to some extent by epistatic gene action.

Regardless of the gene action involved, it should be possible to develop a rye strain which does not possess either type of deleterious gene action. Once such a rye is developed, it could be used in the synthesis of triticale. Hence, a breeding program with this objective is proposed (Figure 3).

The proposed program is basically one of recurrent selection with the objective of reducing the specific combining ability for sclerotium number, average sclerotium weight or total sclerotia weight in wheat x rye crosses. Accordingly, specific combining ability is assessed by test crossing a rye such as line 127 to a *T. timopheevi* tester. By using the 4B288 *timopheevi* as a tester, the rye genome is evaluated in a wheat background in which any dominant and/or epistatic gene actions can be expressed. Selfed seed of each rye plant is automatically produced from bagged heads. Consequently, once the wheat x rye crosses have been inoculated with *C. purpurea*, and the disease reactions evaluated, a population can be reconstituted with the rye plants which conditioned the least susceptibility in the wheat x rye crosses. If sibbing is used to reconstitute the population, it should be possible to make progress against the specific combining ability effect as the frequency of the resistant recessive genes should slowly increase in the rye population and the undesirable linkage to epistatic genes should be broken.

One problem that will be encountered in such a recurrent

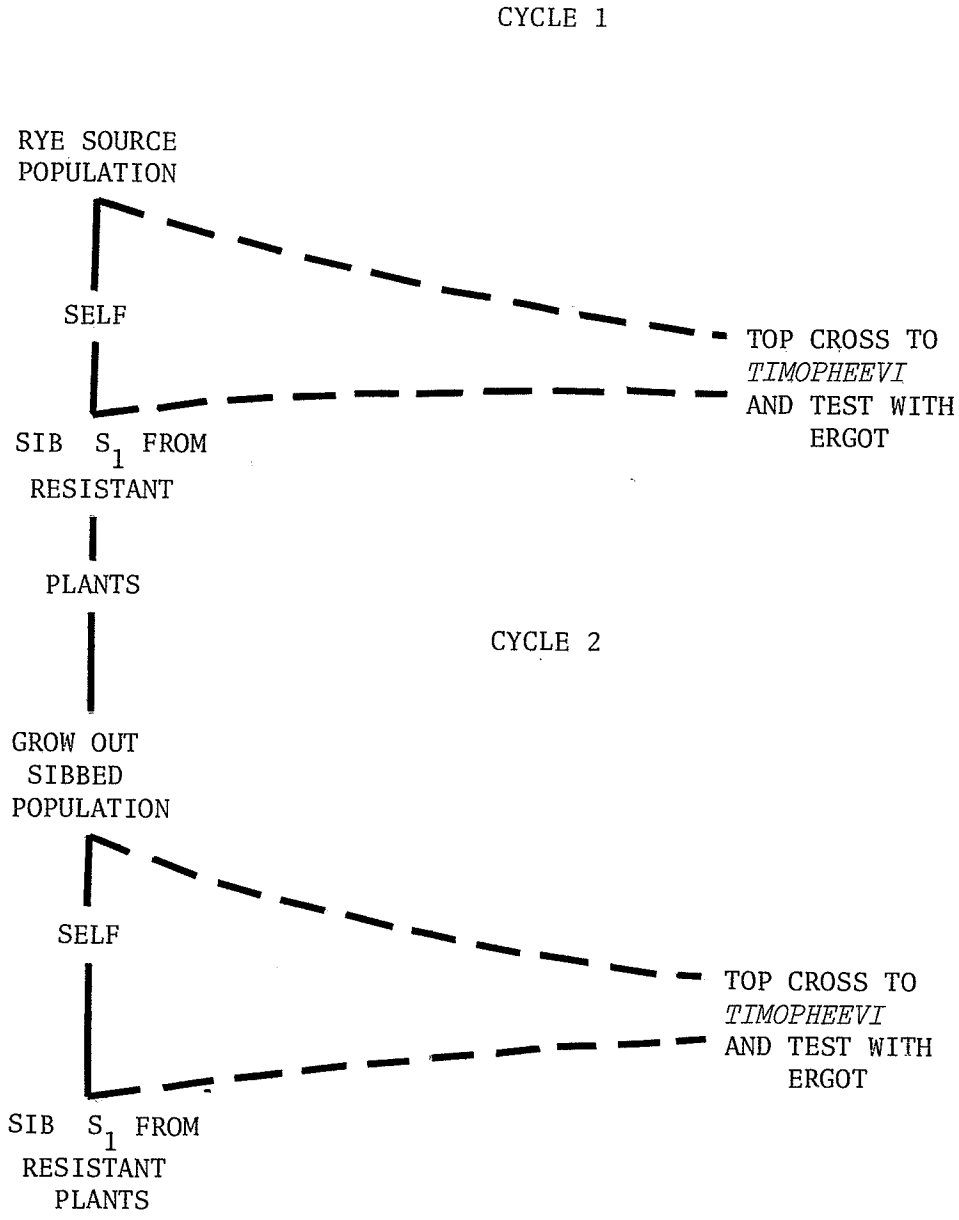


Figure 3. Proposed breeding system for the development of ergot resistant *T. timopheevi* x *S. cereale* crosses

selection program is the selection of the ergot isolate to be used in the screening process. If it is assumed that races occur in *C. purpurea* such as exist in the rust pathogen, and if different genes condition resistance to each of these races, a broad genetic base will be necessary in triticale. Consequently, if an isolate representative of field inoculum is used to test the recurrent selection material, a wide range of resistance genes should be selected. Resistance achieved in this manner should express itself under field conditions.

SUMMARY

During the course of this investigation the following conclusions were drawn:

(1) *T. timopheevi* x *S. cereale* interspecific crosses can be grown in large numbers by using the recently modified embryo culture techniques (Taira and Larter, 1978).

(2) The resistance of *T. timopheevi* accessions to ergot (*C. purpurea* [Fr.] Tul.) was not fully expressed in the F_1 hybrids and amphidiploids of *T. timopheevi* x *S. cereale* crosses.

(3) Sclerotial frequency and average sclerotium weight were found to be sensitive measures of ergot resistance.

(4) Total sclerotia weight which combines both sclerotial frequency and average sclerotium weight into one measurement was also found to be a sensitive measure of ergot resistance.

(5) The single spore isolate which attacked the *T. timopheevi* accessions differentially was able to parasitize some plants in all the *T. timopheevi* x *S. cereale* and *T. timopheevi* x *T. durum* crosses.

(6) Both general and/or specific combining ability effects were indicated in the various combining ability analyses of the *T. timopheevi* x *T. durum* and the *T. timopheevi* x *S. cereale* crosses.

(7) Resistance of *T. durum* cv. Carleton appeared to be expressed in *T. timopheevi* x *T. durum* hybrids.

(8) No one rye could be recommended for use in further studies without knowing which *timopheevi* accession will form the maternal parent.

(9) The 4B288 *T. timopheevi* accession was thought to be the promising accession when crossed to line 127 rye and Carleton durum.

Based on these conclusions, it will be difficult to develop a triticale in which the *T. timopheevi* ergot resistance can be expressed. Future studies must concentrate, therefore, on trying to develop tetraploid wheat and rye genomes which will allow ergot resistance to be expressed. In order to achieve this objective, new approaches in the breeding program may have to be taken.

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APPENDIX

APPENDIX TABLE 1. Standard errors of difference for paired-t-test differences between isolates for sclerotial frequency, average sclerotium weight and total sclerotia weight for *T. timopheevi* x *S. cereale* data

timopheevi parent	Rye parent	Standard error of difference		
		Sclerotial frequency[†]	Average sclerotium weight	Total sclerotia weight
4B573	UC90	6.37	6.48	38.94
4B286	UC90	3.39	2.86	18.22
4B287	UC90	4.93	3.69	20.68
4B288	UC90	6.02	6.08	19.11
4B289	UC90	4.80	7.04	33.78
4B573	127	5.79	2.77	14.30
4B286	127	6.59	4.27	36.43
4B287	127	5.60	3.14	34.90
4B288	127	6.20	9.25	34.21
4B289	127	4.32	3.55	22.38

[†]arc sine transformed

APPENDIX TABLE 2. Standard errors of difference for paired-t-test differences between isolates for sclerotial frequency, average sclerotium weight and total sclerotia weight for *T. timopheevi* x *S. cereale* data

timopheevi parent	Durum parent	Standard error of difference		
		Sclerotial frequency†	Average sclerotium weight	Total sclerotia weight
4B573	Stewart	4.09	1.40	10.95
4B286	Stewart	4.25	2.11	15.07
4B287	Stewart	3.03	3.24	18.89
4B288	Stewart	3.33	2.12	15.86
4B289	Stewart	3.11	2.92	15.90
4B573	Carleton	1.96	3.04	4.80
4B286	Carleton	2.50	1.98	12.01
4B287	Carleton	3.00	1.61	10.23
4B288	Carleton	3.56	2.21	6.93
4B289	Carleton	3.35	1.94	11.09

†arc sine transformed

APPENDIX TABLE 3. Standard error of the means for sclerotial frequency, average sclerotium weight and total sclerotia weight for *T. timopheevi* x *S. cereale* crosses inoculated with two isolates of *C. purpurea*

timopheevi parent	Rye parent	Standard error of the mean					
		Sclerotial frequency†		Average sclerotium weight		Total sclerotia weight	
		R3A	M15A	R3A	M15A	R3A	M15A
4B573	UC90	8.43	5.08	3.54	4.17	31.34	35.6
4B286	UC90	5.18	3.71	1.62	2.24	3.29	18.00
4B287	UC90	3.99	5.20	4.29	3.83	32.09	29.13
4B288	UC90	7.29	7.43	3.24	3.60	25.68	30.33
4B289	UC90	5.99	5.50	4.71	4.58	27.40	36.16
4B573	127	4.77	2.90	3.96	2.34	19.87	25.45
4B286	127	3.96	5.35	2.92	4.37	29.33	36.97
4B287	127	4.32	5.26	1.43	3.19	9.13	21.94
4B288	127	3.94	5.16	1.63	6.53	3.49	26.99
4B289	127	4.35	4.23	1.60	3.45	10.47	26.09

†arc sine transformed

APPENDIX TABLE 4. Standard error of the mean for sclerotial frequency, average sclerotium weight and total sclerotia weight for *T. timopheevi* x *T. durum* crosses inoculated with two isolates of *C. purpurea*

timopheevi parent	Rye parent	Standard error of the mean					
		Sclerotial frequency†		Average sclerotium weight		Total sclerotia weight	
		R3A	M15A	R3A	M15A	R3A	M15A
4B573	Stewart	3.24	3.24	.91	1.67	4.7	11.61
4B286	Stewart	4.27	3.04	2.08	3.02	5.6	9.50
4B287	Stewart	2.45	2.57	.79	2.52	2.37	10.48
4B288	Stewart	2.23	3.19	.67	2.07	3.52	15.64
4B289	Stewart	2.19	1.88	.49	2.74	1.73	15.05
4B573	Carleton	2.12	2.15	.62	1.39	2.69	3.61
4B286	Carleton	1.67	2.34	.78	1.10	5.66	12.63
4B287	Carleton	2.40	3.59	.72	1.03	2.40	17.52
4B288	Carleton	2.20	3.39	.81	1.75	1.70	6.22
4B289	Carleton	2.11	2.99	.59	1.46	2.37	9.96

†arc sine transformed