Development of additive resistance in wheat, Triticum aestivum L., to stripe rust, Puccinia striiformis West
by Joseph Michael Krupinsky

A thesis submitted in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Plant Pathology
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Abstract:
Gene action of resistance to stripe rust was determined in "minor gene lines" of wheat (P.I. 178383/Itana// commercial variety). When the minor gene lines were intercrossed, a high level of resistance was maintained in the F2 and the F3 segregating progeny. Additive gene action and high heritabilities, which were demonstrated by two dialled analyses of advanced minor gene lines, indicated that this resistance could be manipulated easily in a breeding program.

Ten acceptable commercial varieties of spring wheat with resistant, intermediate, and susceptible reactions to stripe rust were intercrossed. Ten winter wheats, also acceptable commercial varieties, with intermediate and susceptible reactions were intercrossed. The most resistant seedlings (10 to 20 percent) were selected in each segregating generation, transplanted and grown to maturity.

Results with 43 spring wheat crosses and 38 winter wheat crosses evaluated as seedlings in controlled environmental chambers demonstrated selection for transgressive segregation. In the field, progress towards increased resistance was demonstrated with 35 winter wheat crosses. Transgressive segregation was demonstrated in later generations for nine spring wheat crosses and 31 winter wheat ' crosses which lacked resistant progeny in the F2 and F3 generations. Thus, resistance was selected from parents which had intermediate and susceptible reaction types.

The selection of resistance from crosses among susceptible varieties was demonstrated. These appear to be new sources of resistance which have been overlooked or selected against in the past. Once such resistance was built up, it could be manipulated as demonstrated with the additive, minor-gene lines. On the basis of infection results with several different virulence components in the pathogen, this resistance is believed to be of a general or non-specific nature.

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ABSTRACT

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INTRODUCTION

The stripe rust disease of wheat, *Triticum aestivum* L., caused by *Puccinia striiformis* West., is found on all continents of the world except Australia (122). Stripe rust is the most widespread and important rust disease of wheat in North-West Europe (57), and it has assumed a role of major importance in the Near East as evidenced by the destructive epidemics of the 1960's (107). Great economic losses in the Pacific Northwest Region of the United States were caused by the disease in 1960-64 and moderate damage has occurred since then (35). The use of wheat varieties resistant to stripe rust as a control method was proposed in 1924 (40) and is still the most feasible means of control (37). Specific resistance has been the major type of disease resistance used (31). But more recently, a general type of resistance has been developed (96, 99, 108).

In 1963 several fourth-backcross lines from susceptible parents -- Norin 10-Brevor 14 and Burt - were moderately resistant to infection by *P. striiformis*, an example of transgressive segregation. Allan *et al.* suggested that complementary gene action was involved in the expression of resistance within these backcross lines (4). Transgressive segregation for adult resistance to stripe rust was encountered again in a cross of Itana x Burt in 1966 (2). W. K. Pope and W. L. Nelson made similar observations in progeny of crosses involving Itana (2). Pope reported transgressive segregation for resistance to stripe rust and concluded that at least 20 genes were present in susceptible wheats which might confer partial resistance to progeny of appropriate crosses (70, 71). At about the same time, Sharp was studying the effect of temperature on the infection process of *P. striiformis* (89, 90, 91, 92). These studies provided the methods and techniques for distinguishing the major and minor genes in P.I. 178383 (98, Sharp, personal communication 1966).

Lewellen *et al.* studied the inheritance of both major and minor genes for stripe rust resistance by crossing P.I. 178383 with Chinese 166 and Lemhi and by using two temperature profiles. The presence of minor genes was clearly demonstrated in F_3 plants at the 15/24 C temperature profile. These F_3 plants were from F_2 plants which had been selected with susceptible infection types at the 2/18 C temperature profile in order to avoid including the major genes. These minor resistance factors were typically quantitative in their behavior and when brought together in certain combinations they showed transgressive segregation.

Thus, these minor resistance factors in P.I. 178383 acted in an additive manner to condition host-parasite incompatibility (49, 51). From this and more recent work, it can be concluded that the minor genes: 1) behave as recessives, 2) are temperature sensitive, 3) confer higher levels of resistance when added together, 4) are possibly found in many commerical wheat cultivars, and 5) are a possibility of providing a long-lasting general resistance (94, 95, 96, 99, 100).

The general nature of this resistance was reported by Stubbs who has worked with four minor gene lines of Sharp (108). Sharp has also demonstrated the general nature of this resistance by testing these additive minor genes with four races from the United States and five races from Europe (Sharp, personal communication).

In recent years, there has been an increasing recognition of the importance of general resistance in controlling plant diseases. Although many studies have recently been initiated to develop methods of determining general resistance, little information is currently available on the inheritance and manipulation of polygenic resistance usually associated with general resistance. The additive, minor-gene resistance is one example where general resistance has been demonstrated at the present time. Thus, the genetic material for studying general resistance is available.

This thesis is a further study of these additive, minor-gene lines and was undertaken in order to determine the gene action associated with this form of general resistance and to decide whether this resistance can be manipulated in a regular breeding program once it is obtained. The second part of the thesis was undertaken to see if an additive, minor-gene resistance can be obtained from agronomically acceptable wheats. The use of commercially acceptable cultivars as parents would reduce considerably the undesirable traits usually associated with various plant introductions which are the usual sources of resistance. This objective was pursued by intercrossing intermediate and susceptible winter wheats and by intercrossing resistant, intermediate, and susceptible spring wheats, and selecting the most resistant progeny of each generation.

LITERATURE REVIEW

Early History

Stripe rust on wheat was first described by Schmidt in 1827 as *Uredo glumarum*. In 1894 Eriksson and Henning described the telial stage of the fungus and transferred the species to the genus *Puccinia* (40). The first report of stripe rust in the United States was by Carleton in 1915 (16). He reported that Dr. F. K. Raven from Copenhagen, Denmark, had identified *P. striiformis* on wheat near Sacaton, Arizona, and that A. G. Johnson had found stripe rust on *Hordeum murinum* in Southern California at about the same time. In 1924 Humphrey *et al.* reported that the disease was distributed from British Columbia to Mexico and eastward to 103° west longtitude and that it was present in all Pacific and intermountain states (40).

Although Farrer (1889) stated that susceptibility to rust was hereditary in wheat (8), Biffen was the first to demonstrate the heritability of stripe rust resistance. In 1902 he crossed Red King *(Triticum aestivum)*, a very susceptible wheat, with Rivet Wheat *(Triticum turgidum)* which was resistant. The F_1 plants were all susceptible but the F_2 progeny gave a 1:3 ratio (64 immune and 195 susceptible).

> "Now the ratio 64:195 seems to be too close an approximation to the ratio 1:3 to be mere accident, and taken in conjunction with the fact that the F_1

> generation was so badly attacked it is fair proof that susceptibility and immunity are definite Mendelian characters, the former being the dominant one." (8)

Thus, the inheritance of immunity and susceptibility to parasitic fungi could be followed as readily as that of morphological characters (9). A rather complete review of the early works on stripe rust on wheat as well as recent work has been written by Hassebrauk and Robbelen (31).

Puccinia striiformis, the Organism

Puccinia striiformis West. has had several different names: *Uredo glumarum* J. K. Schmidt, 1827; *Puccinia straminis* Fuckel, 1860; *Puccinia neglecta* Westend, 1863; *Puccinia glumarum* Erikss. and Henn., 1894; *Puccinia lineatula* Bub., 1914; and *Puccinia stapfiolae* Mundk. and Thirum., 1946 (20). Two common names for *P. striiformis* are in present usage -- stripe rust in the United States and yellow rust in Europe. No aecial stage of the organism is known (20). Nuclei of *P. striiformis* measure 4.6 x 3.4 µm. Chromosome length is 0.7 - 1.1 µm which is comparable to other *Puccinia* spp. Six chromosomes have been observed suggesting that *P. striiformis* is heterothallic since other heterothallic species of *Puccinia* have six chromosomes (27).

Stripe rust is more sensitive to environment than other cereal rusts (33, 58, 64). Most of the early work concerning the biology of stripe rust urediospores was done in Germany by Straib (105) and Stroede (106). The germination of stripe rust urediospores is determined by their generation constitution (33), environmental conditions during their development (33, 64), conditions during their storage (64), and conditions during germination (33, 64). Many factors that influence spore germination were studied by the early workers in Germany and were reviewed by Hassebrauk (30) and Schroder and Hassebrauk (86). A number of these factors are: light (63), ultraviolet radiation (59), temperature (15, 33, 63), and atmospheric conditions such as CO_2 levels (58), tobacco smoke (65), ionization (93), atmospheric pressure changes (86), and relative humidity (33, 77). Also, the number of stripe rust spores present in a germination field may have an influence. No mutual interference of germination was found with 100 to 8,000 spores/cm^2 whereas higher spore densities resulted in proportionally increasing self-inhibition of germination (111). Rapilly found that spores in groups germinate better than isolated spores and that the size of the group increased with relative humidity (77).

Optimum temperatures for germination vary among isolates of *P. striiformis:* 4-8 C (26), 9-12 C (86), 10-13 C (60), 15 C (86), and 22.5 C for one race (60). The reason for variation may be that the temperature during urediospore production governs the maximum germination temperature of the spore (86, 110). Temperature changes involving the host during the infection process or even prior to inoculation can cause significant changes in the infection type produced (92).

Epidemiology of *Puccinia striiformis*

The epidemiology of stripe rust has been studied in the United States (15, 40, 88, 112), Europe (26, 32, 124), China (54), and many other countries. Reviews by Zadoks (124) in which he surveyed the literature of about 200 papers on rust and Hassebrauk and Robbelen (32) are good sources for more detailed information on the subject. In general, three factors are necessary for an epidemic: a susceptible host, viable spores of an aggressive race of the pathogen, and favorable environmental conditions.

Numerous reports on the overwintering and oversummering of stripe rust are found in the literature. Sharp and Hehn (97) reported that stripe rust has the ability to survive any winter that wheat foliage survives. The fungus can survive as uredomycelium in the host for 3 to 5 months, especially under snow (122, 124). Viable urediospores can persist on desiccated host tissue and cause infections when new foliage is available. Stripe rust urediospores can germinate at temperatures as low as -4 C (15). During the summer, urediospores can survive on dry stubble for at least 51 days and on dry soil for up to one month when the mean maximum temperatures are in the range of 25-30 C (87). In California, the fungus reportedly oversummers on wild grasses at altitudes of 6,000 feet or above. Viable urediospores can then be disseminated by wind and transported in one step a distance of at least 150 miles (112). Tu has demonstrated that infection can occur during any summer night at Pullman, Washington, when susceptible host, viable urediospores and adequate moisture are present. He exposed greenhouse grown wheat seedlings to an open field environment each night from August 7 to September 5, 1964, and established the fact that inoculum is present in the environment and that natural infection can occur when at least three hours of rain or dew is recorded (115).

Loss of Wheat Crops due to *Puccinia Striiformis*

References to yield loss due to stripe rust are numerous. Although Stubbs reported losses from 0 to 100 percent, he stated that a general estimate of yield loss would be 25 to 50 percent since most figures fall within that range (107). Major losses to stripe rust in the Pacific Northwest occurred in 1960, 1961, 1962 and 1963 (2, 72). Losses in wheat due to stripe rust in Europe are well documented in the literature. In 1965, Zadoks listed the dates of the stripe rust epidemics and the damage caused in 14 countries: Belgium, Czechoslovakia, Denmark, France, Germany, Netherlands, Norway, Portugal, Romania, Spain, Sweden, Switzerland, United Kingdom and the U.S.S.R. (124). Stripe rust has also been classified as a destructive rust fungus in several other countries: Colombia (11), Kenya (19), Iran (45), India (44), and China (54).

A reduction in yield from a rust infection is generally proportional to the degree and duration of infection (22). Yield losses can be attributed to retarded growth and vigor of the plant (7, 22), reduced production of roots (7, 22), reduction in tiller number (4, 34), reduction in size and number of heads (7), reduction in number of florets per head (22), reduction in size and number of kernels (7, 22), reduction in total dry matter (7), and altered metabolism of the host plant (22, 61, 62).

Physiological Races

Since the literature contains numerous studies concerning physiological races of *P. striiformis,* no attempt will be made to summarize this voluminous subject matter. Hassebrauk and Robbelen have provided the most recent summary of physiological races (31).

In the United States, Bever, by distinguishing an Idaho and Montana type of stripe rust, was the first to report different physiological races (6). In 1963 Purdy and Allen distinguished three distinct physiological races in the western United States (75). In 1969 a new race was found on Moro (5) which contains only the major resistance gene from P.I. 178383 (100). Line *et al.* proposed a flexible system for differentiating virulences of *P. striiformis* isolates in the United States (53). In 1972 Line reported four races of stripe rust of potential importance in the United States, PNW 1, PNW 2, PNW 3 and PNW 5 (52). Volin and Sharp surveyed the northwestern United States for physiological races of *P. striiformis* in 1973. They observed that the European differential set was not adequate to differentiate the genes for virulence prevalent in the northwestern United States. With a new set of differentials, it was possible to differentiate 11 pathotypes, tentatively designated as MAES (Montana Agricultural Experiment Station) 1 through 11 (118).

Genetic Resistance

Introduction. As early as 1924 the adoption of wheat varieties resistant to stripe rust was recommended as the most practical means of control (40). The classification of types of resistance to rusts has been somewhat arbitrary. Some workers have classified rust resistance into morphological, functional, and physiological types whereas others have used the terms physiological resistance, stage resistance, adult plant resistance, combined resistance, overall resistance, generalized resistance, heat resistance, and field resistance (37). Resistance to rust fungi has been divided into two types when the physiological specialization of the pathogen is considered: specific resistance which functions only against certain rust races or biotypes and generalized resistance which functions against all biotypes (37). These two types of resistance are referred to as vertical and horizontal resistance by Van der Plank (116). Other discussions on the meaning of and the genetics of disease resistance in plants have been presented by Nelson (68), Robinson (78, 79, 80), Day (21), Williams (120), Hooker (37, 38), Abdalla and Hermsen (1), Simons (101), and Schafer (84).

In general, rust control may be expressed in various ways and at different stages of the host development. Manners (62) lists the best known types as: 1) seedling resistance, when a variety is resistant to a particular race as a seedling and a mature plant; 2) mature or adult plant resistance when the seedling is susceptible but the mature plant is resistant; 3) environmentally controlled resistance, when temperature is the most important factor concerned; for example, high temperatures increase resistance to *P. striiformis;* and 4) tolerance, when the plant appears susceptible but the yield is only slightly affected.

The literature contains many studies on the physiological specialization in rust fungi involving the hypersensitive type of resistance in which segregations are usually discrete and fit simple genetic ratios (37). Little is known about the inheritance of generalized resistance or tolerance. The most comprehensive review on the genetics of resistance to stripe rust is presented by Hassebrauk and Robbelen (31).

Tolerance. Tolerance refers to the ability of a susceptible host to endure severe attack by a pathogen without sustaining severe losses in yield or quality. The term, tolerance, should not be confused with intermediate degree of resistance (18). Tolerance should be more stable than hypersensitivity-induced resistance (18, 47, 84, 101). From the standpoint of stability over time, tolerance should be superior to resistance because new forms of the fungus that may arise would not have a selective advantage over existing forms of the fungus (101). Although tolerance has been mentioned as a potential control method for stripe rust, to date no tolerance studies have been reported.

Specific resistance. Specific resistance is effective only against certain populations of a pathogen but not against others (17, 37). Many different names have been used to describe this type of resistance: differential, major, monogenic, oligogenic, physiologic, seedling, hypersensitivity, major-gene, racial, race specific, vertical, special resistance, non-uniform (1, 17, 67, 116, 120). Specific resistance genes in the host plant function by restricting the infection site and the infection process of the parasite (67). This type of resistance delays the start of an epidemic and contributes a defense mechanism against specific races (1). It is usually monogenic or oligogenic, e.g., being controlled by single, dominant genes that act independently of one another (17, 47, 120). Specific resistance is excellent as long as it remains effective but in general it has been of short-lived usefulness, although there are notable exceptions (1, 17, 47, 119).

Unfortunately, specific resistance places the pathogens that are not pathogenically stable under extremely severe selection pressure. The pathogen then undergoes rapid evolutionary changes and only the individuals with the corresponding gene for virulence can compete on the cultivar (47). In the 30 years since the release of rust resistant varieties, it has become rather obvious that the adaptation of the cereal rusts to these varieties is the rule rather than the exception (43).

There are many examples of resistance genes being overcome by new races of *P. striiformis*. In the Pacific Northwest a single dominant factor for resistance was reported in the cultivar Suwon 92 (3) which was later heavily attacked by a new race (76). The major gene from P.I. 178383 in the variety Moro, C.I. 13740, was overcome in a similar fashion (5).

In Columbia all stripe rust resistant varieties have become, with one exception, susceptible within five years of their release (11). In England, there have been severe epidemics over the last ten years on at least eight varieties which were resistant to all known races of *P. striiformis* when they first entered the national trials (10). Feekes concluded that the value of breeding resistance to specific races has been overestimated for the last 15 years since such specific resistance for stripe rust is temporary. A new cereal variety may be struck down by a new physiological race even before obtaining widespread acceptance (23).

A number of workers have proposed that multiline varieties and hybrids or a large number of varieties, each with a different specific gene, be grown in a geographic region (1, 14, 37). Borlaug has proposed the multilineal hybrid variety as the best means of obtaining a long-lasting rust resistance in a commercial wheat variety (11). The multiline will curb racial shifts of the pathogen, and it is unlikely that a race could acquire all the necessary virulence genes to match all the specific genes (14, 67). In Columbia, multiline cultivars -- Miramar 63 and Miramar 65 -- have been developed for commercial use (13). Released in an area where stripe rust was a serious problem, Miramar 63 has buffered effectively against losses from stem and stripe rust (14).

Nelson suggests that multigenic cultivars with pyramided genes, e.g., specific genes functioning collectively in a single genetic background, would be superior to multilines (67). A variety with multigenic specific resistance would provide more than one physiological barrier in each plant against infection. This would avoid a stepwise development of races virulent to varieties possessing different single genes. Simultaneous mutations or recombinations of mutations for virulence to all specific genes involved appears unlikely (83). This also assumes that new genes would not be released singly (46).

The use of moderate specific genes (intermediate reaction) has been proposed by Knott. He states that a high degree of disease resistance is often not essential and that the use of moderate specific resistance would not put the pathogen under severe selection pressure. Thus, the selection pressure in favor of more virulent races is greatly reduced. The concept needs to be tested further (46, 47).

General Resistance

Introduction. General resistance is a race nonspecific resistance which functions against all biotypes or races of a pathogen (37). It is the resistance "that experience and adequate testing in nature have shown to confer an enduring and stable protection against a pathogen or disease" (17). In many cases, it is difficult to prove a given form of resistance is general. Thus, a resistance can be regarded as general until further work proves otherwise (37). General resistance has many different names: uniform, polygenic, multigenic, minor gene, partial, generalized, race non-specific, horizontal, field resistance, durable, and adult plant resistance (1, 10, 17, 102, 116, 120). Thurston in his review of general resistance to *Phytophthora infestans* alone has listed 15 different terms used for general resistance (109).

The use of general resistance may form a host-parasite balance which would minimize the development of new races (1). This resistance functions equally against all races by reducing the amount of disease or by slowing the disease increase. Several different genetic changes in the pathogen are probably needed to overcome a general resistance that is polygenic in nature. Thus, the probability that any given race might acquire, accumulate, and maintain all the necessary virulence genes is lessened (67, 68).

General resistance is often controlled by multiple genes with additive effects (47, 102). The heritability of general resistance to cereal rusts has been studied only for a short time and is considered to be controlled polygenically (102, 103). This resistance is difficult to study and use because it is affected by many factors and environmental conditions which cause variations in its expression and inheritance. Thus, it is generally considered to be difficult to incorporate into host varieties (1, 47).

General resistance can take many forms and be variable in its expression and inheritance (47). Thus, as Abdulla and Hermsen have stated, cereal breeders show little interest in general resistance (1). A system for development of general resistance would probably involve the mass selection or recurrent selection techniques of plant breeding (102). Recurrent selection has been used effectively in corn breeding for developing general resistance to northern leaf blight caused by *Helminthosporium turcicum* (41) and corn rust caused by *Puccinia sorghi* (38). Goode and Bowers were able to develop multigenic resistance to anthracnose in cucumber caused by *Glomerella cingulata* var. *orbiculare*. They inoculated the progeny of each cross and selected the resistant plants for the parents of the next generation (28).

The general resistance to late blight of potatoes, caused by *Phytophthora infestans* (Mont.) de by., is considered a classic in the history of disease resistance (17). This resistance has demonstrated acceptable stability in ten years of field trials in Mexico. In some selected cultivars, there may be an erosion of the resistance but no sudden breakdown (69). The resistance appears to be a complex of many factors governing the penetration, spread, multiplication and reproduction of the parasite: Reduction in the rate of penetration and colonization of the host, reduction of lesion size,increase in time required for sporulation, and reduction in the quantities of sporangia and zoospores produced (25, 29). The degree of resistance is governed by a series of minor genes (113, 114). Rather than spending more time on this subject at the present time, the reader is referred to the short review by Simons (102) or the more detailed review of 88 papers by Thurston (109) for information on general resistance to *P. infestans*.

Another good example is general resistance to corn rust, caused by *P. sorghi*, which is distributed throughout the world and is endemic on corn in the Western Hemisphere. The rust fungus which is composed of many biotypes or physiologic races is usually present each year in the Corn

Belt, but it is considered to be of little importance. The reason for this is the presence of a mature plant type resistance. Even though the resistance is polygenic in inheritance, it can easily be selected for in a breeding program since it has a heritability of 85 percent (37, 38).

Stripe rust. General resistance against stripe rust has been mentioned in the literature for a number of different varieties, but it has not been demonstrated to the extent of the above examples. In Denmark, Hermansen noted varieties that are susceptible but act as poor spreaders under field conditions. He concluded that these varieties, grown for 25 or more years, possess some degree of general resistance which is of economic value under conditions there (36). Slovencikova in Czechoslovakia has reported that the Chlumecka '12 and Ebrovicka '10 resistance has lasted over 48 years but breaks down to a susceptible reaction in the greenhouse with short days and 13 C temperatures (104). A non-specific resistance from Karlik, a short Bezostaia type wheat, has been reported in Romania (66).

The adult-plant resistance of the commercial wheat varieties -- Little Joss, Holdfast, Browick, and Cappelle-Desprez -- is considered to be a durable, stable, or dependable resistance by Russell (82). The cultivar, Hybride de Bersee, is mentioned by Johnson and Law as having adult-plant resistance (42). Lupton lists the commercial varieties -- Little Joss, Atle, and Maris Widgeon -- as having mature-plant resistance (56). From these examples, adult-plant resistance appears to be a stable general resistance. Thus, many lines are selected for adult-plant resistance, and there is usually no objection to varieties with adult-plant resistance and seedling susceptibility (123). However, it is generally overlooked that this mature-plant resistance breaks down when a new and compatible rust race appears (17, 123); for example, the adult-plant resistance of Maris Huntsman (74).

A slow-rusting variety is one on which the percentage of rust infection increases more slowly than it does on a susceptible variety (37, 55). Reviews of this resistance are presented by Hooker (37) and Simons (102). Slow-rusting resistance for stripe rust has not been studied until recently. Priestly reported that using the Wycombe seedling method for detecting differences for susceptibility or slow-rusting, high correlations can be found between seedling and adult field assessments (73). Young and Powelson in their studies on the quantitative host-pathogen responses were able to detect differences in factors affecting nonspecific resistance: 1) germination and penetration, 2) latent period, 3) infection type, 4) spores produced per unit lesion area, 5) infection period, and 6) rate of disease increase (121). Russell studied both disease escape and reduced sporulation on several varieties. No varieties examined had disease escape (reduced spore deposition, germination and penetration), reduced growth and reduced sporulation. He speculated that more satisfactory resistance might be obtained by combining all these resistance characters into one variety (81).

Additive minor-gene resistance is a type of general resistance which depends on a number of genes which by themselves confer little resistance, but when utilized together, confer a high level of stable resistance. Sharp and Pope's finding of minor genes which express themselves in the absence of major genes, has "contributed a great breakthrough in our knowledge of the genetic background of disease expression" (107). In 1965 Pope stated that a

> "number of wheats that are classified as susceptible do carry genes which while not doing much that is visible in that particular wheat, do contribute something useful to some segregates in appropriate crosses." (70)

He reported that there is a large number of genes, 20 or so, which give only partial resistance. More recently, Henriksen and Pope showed segregation of minor genes for additive levels of resistance (35).

Sharp and Hehn reported the presence of major and minor genes which condition resistance in P.I. 178383 (98). Under environmentally controlled conditions, Lewellen (49) and Lewellen *et al.* (51) showed that these minor factors were inherited in an additive manner and were temperature sensitive. The minor genes expressed their greatest resistance at the relatively higher temperatures. The inheritance of minor gene combinations were further studied at two temperature profiles by Lewellen and Sharp (50). They considered the differences in sensitivity to temperature to be due to different physiologic responses of the minor genes concerned. Work by Brown and Sharp showed that short exposures to contrasting temperatures for as little as four hours at certain phases in the infection process resulted in significant changes in infection type (12).

The additive minor genes were tested for specificity or nonspecificity by Sharp and Volin. They demonstrated that wheat lines containing minor genes from P.I. 178383 and Itana showed similar levels of resistance to 11 cultures of *P. striiformis* which contained different genes for virulence. The results indicated that the additive minor genes were non-specific in action, but they also cautioned that this holds for any resistance gene until new genes for virulence appear in the pathogen (100). Stubbs has found that these minor gene lines continue to show general resistance after being in the International Stripe Rust Nursery for ten years during which time they were undoubtedly exposed to numerous virulence genes (108).

These minor gene lines were then crossed with other susceptible winter wheat cultivars. Higher levels of resistance were found in the progeny due to the additional minor genes found in these susceptible cultivars. The resulting transgressive segregation in the F_2 and F_3 from the additive minor gene combination was proposed as a method in developing cultivars with general resistance to stripe rust (95). With more generations of selection and selfing, the F_5 and F_6 lines were very resistant and a number of wheat lines were developed that showed uniform resistance to isolates of *P. striiformis* (96, 99). These minor gene lines were also subjected to the seven major virulence races of *P. striiformis* in the United States and Europe and they showed a general resistance to all races (Sharp, personal communication).

About ten years ago, Caldwell stated that

> "hypersensitivity resistance to a rust that functions as a general type would be both a highly valuable and unique phenomenon in rust resistance" (17).

At the present time, all facts indicate that this has been accomplished by the combination of these additive minor genes for stripe rust resistance. This is a rather controversial statement since hypersensitive resistance against the compound interest diseases in crops grown in uniform stands is considered to be rather unstable (116). It is considered better if the general resistance is not so strong that the pathogen cannot survive (47).

MATERIALS AND METHODS

General Procedure

Seeds were planted in one row down the center of 10.5 cm clay pots which contained steamed soil. The pots were then placed in a walk-in environmental growth chamber. The normal evaluation environment was 15/24±1 C (dark/light) with a 12-hour photoperiod per day (2.2-3.3 ergs/cm^2/sec). Plants were inoculated when the second leaf appeared -- 10 to 12 days after planting. Segregating populations were inoculated with field collections of *P. striiformis* which consisted of two races indigenous to the Gallatin Valley of Montana, tentatively named race 3 and 4, respectively, by Volin (117). For inoculation the plant leaves were horizontally oriented in a modified settling tower. Urediospores were shot up into the tower with a CO_2 gun and allowed to settle for 4 minutes (92). After inoculation, the plants were placed in a dark dew chamber for 20 to 24 hours at 7 C. The plants were then returned to the growth chamber. After one week, the leaves above the primary leaf were clipped off. Disease readings generally were made after an incubation period of 14 days. The 10 infection types of Brown and Sharp (12) were used. These are: resistant types, $\overset{v}{0}0$ (vague chlorotic flecks), 00 (small chlorotic lesions), 0- (chlorotic or necrotic lesions not spanning the width of the leaf), 0 (chlorotic and necrotic lesions spanning the width of the leaf), 1- (very few uredia, chlorosis and/or necrosis); intermediate types, 1 (few uredia, chlorosis and/or necrosis), 2 (uredia, some chlorosis and/or necrosis); and susceptible types, 3- (uredia, traces of chlorosis and/or necrosis), 3 (uredia slight chlorosis), 4 (uredia, no chlorosis). These infection types were assigned numerical values of 1 to 10, respectively (12) in order to facilitate their analysis by computer. In the experiments concerned with selecting additive minor gene resistance, the most resistant individuals (10 to 20 percent of the total) were selected in each generation, transplanted, and grown to maturity to produce seed for the following generation.

The hybrid progeny (F_1) and the parents of 2 diallel crosses were used to study the genetics of resistance of several different groups of material. Because of the large number of replications, weighted means of the infection types were calculated. The number of individual plants for each infection type was multiplied by the infection type value (1 through 10), added together, and divided by the total number of individuals. The data from F_1 hybrids and parents were analyzed by use of the general least squares analysis of diallel experiments developed by Schaffer and Usanis (85). All data from the 2 diallel crosses were analyzed by Davis, Smith, and Kling at the Data Systems Application Division, ARS, USDA, Beltsville, Maryland. From information in the diallel analyses, estimates of gene action, genetic variance and heritability were made according to the methods of Finkner *et al.* (24).

Field Work

All crossing of wheat plants used in this study was done at the Agronomy Field Laboratory, west of Bozeman, Montana. Standard plant breeding techniques for hand emasculating and pollinating with a pollen shower were used. All heads used for crossing were bagged after emasculation. Heads with hybrid seed were harvested and threshed individually. Individual crosses will be identified later.

In 1975 and 1976 stripe rust disease readings on segregating F_2 and F_3 plants were made in the field. Five 10-foot rows of space-planted segregating material were planted between rows of the parents. Susceptible rust spreader rows separated parents of different groups. Itana was the winter wheat spreader, and Lemhi was the spring wheat spreader. Spreader rows surrounding the nursery were inoculated with races 3 and 4 early in the spring in order to insure adequate development of rust. Rust symptoms were read on individual plants. Plants were classified as susceptible, intermediate, or resistant. The susceptible plants had high densities of uredia and prominent striping of the leaves. Plants exhibiting intermediate reactions had moderate numbers of uredia and restricted striping of the leaves. Resistant plants had no uredia or few uredia with restricted striping.

PROCEDURES AND RESULTS

I. Intercrossing of Minor Gene Lines (P.I. 178383/Itana// Commercial Wheat Variety)

Introduction. By inoculation, selection, continuous selfing, and diallel cross-analysis at various temperature regimes, lines of P.I. 178383/Itana were isolated which contained one, two and three minor genes (94, 98). These minor gene lines of P.I. 178383/Itana showed similar levels of resistance to 11 cultures of *P. striiformis* known to possess different genes for virulence (100). These minor gene lines were then crossed with commercial wheat varieties. Intercrossing of the new minor gene lines (P.I. 178383/Itana// Commercial wheat variety) was undertaken to obtain additional information on the gene action of this type of resistance and to determine if it can be manipulated in a breeding or variety development program.

Materials and methods. In 1973, six minor gene lines (P.I. 178383/Itana//Commercial wheat variety) which had one detectable minor gene and six minor gene lines which had two detectable minor genes were selected because of uniform seedling reaction types in the F_4 (Table 1) (Sharp and Sally, personal communication). The lines were crossed in a diallel manner in 1974 to determine if there were

Table 1. Minor gene lines (P.I. 178383/Itana//Commercial wheat variety) intercrossed in 1974.

			Disease Ratings			
			Seedling[1/]	Field[2/]		
Row #	Code	Pedigree		%R[3/]	%I	%S
2876	54-A-1	1^{18} x Lancer	(00)[4/]	100		
2892	64-B-1	1^{18} x Itana	(00)		100	
2898	65-A-2	1^{18} x Wanser	(00)	100		
2916	68-A-1	1^{18} x Delmar	(00)		86	14
2903	66-A-3	1^{18} x Rg/Cnn 37-3-6	(00)	97	3	
2909	67-A-1	1^{18} x /3/NB17-6/ Y-18-18-1//YTO/ 7-1-1-4-3	(00)		100	
2826	90-A-1	2^{14} x Gaines	(00)	59	40	
2862	96-A-Z	2^{15} x Gaines	(00)	37	52	11
2839	92-A-1	2^{14} x Itana	(00)	48	36	15
2816	101-A-1	2^{17} x Itana	(2)		19	81
2858	95-B-1	2^{15} x McCall	(00)		61	39
2819	104-A-1	2^{17} x Delmar	(00)	100		

[1] 1973 F_4 readings.
[2] 1974 F_5 readings.
[3] R = resistant, I = intermediate, S = susceptible
[4] Infection type, see page 27.

differences in the minor genes present. The lines with one detectable minor gene were intercrossed in a 6 x 6 diallel, crosses number 101 through 130. The lines with two detectable minor genes were intercrossed in another 6 x 6 diallel, crosses number 131 through 160.

Results and discussion. Unfortunately, the lines were not yet completely homozygous under field conditions even though they appeared to be in the F_4 (Table 1). Because of the variation in the F_5 of lines with two minor genes, no further study of the crossed material was undertaken. Although the variation in the F_5 of the lines with one minor gene was much less, no attempt at a diallel analysis was made. Only six crosses in which stable lines were used as parents -- 101 (1/Lancer//1/Itana), 104 (1//Lancer///1//Rg/Cnn 37-3-6), 106 (1/Itana//1/Lancer), 109 (1//Itana///1//Rg/Cnn 37-3-6), 121 (1//Rg/Cnn 37-3-6/// 1//Lancer), and 122 (1//Rg/Cnn 37-3-6///1//Itana) -- were studied further to determine if the resistance of the minor gene lines could be manipulated after crossing. The combinations studied were resistant/resistant (104 and 121), resistant/intermediate (101 and 122), and intermediate/ resistant (106 and 109).

The F_2 and F_3 progeny from the resistant/resistant crosses 104 and 121 were mostly resistant (Table 2). The progeny from the resistant/intermediate crosses (101 and 122) were slightly more resistant than the intermediate/resistant crosses (106 and 109); perhaps a slight maternal effect was involved. But in general 90 percent of the progeny from the intercrossed minor gene lines were resistant even though an intermediate type was used in 4 of the 6 crosses. Thus, additive minor gene resistance was not lost after crossing but was maintained and easily manipulated.

II. Further Intercrossing of Minor Gene Lines (P.I. 178383/Itana//Commercial Wheat Variety)

Materials and methods. The F_1 plants of the 6 crosses studied above -- 101, 104, 106, 109, 121 and 122 -- were intercrossed to obtain the hybrids numbered 233 through 243. These 12 crosses were made to determine how additive minor gene resistance reacts when 4 parents are involved ($P_1/P_2//P_3/P_4$).

Results and discussion. The results obtained were very similar to those with 2 parents. Considering the F_1 and F_2, 89 percent of the progeny were in the resistant class, 9 percent in the intermediate class, and 2 percent

Table 2. Results obtained from intercrossing minor gene lines (P.I. 178383/Itana//Commercial wheat variety) and selection for resistance in the F_2 generation.

Cross number	Generation	Number of plants for each infection type									
		Resistant					Intermediate		Susceptible		
		v	00	0-	0	1-	1	2	3-	3	4
101 (RxI)[1]	F_1				3	2	2				
	F_2		2	21	39	14	10	2			
	F_3			35	137	11	8	18	2		
104 (RxR)	F_1				1						
	F_2	18	18	37	43	1	1	1			
	F_3	8		62	132	1	1	1			
106 (IxR)	F_1			2	3		3	1			
	F_2	3	1	19	41	11	15	2	2	2	
	F_3	2		35	103	7	11	20	4		
109 (IxR)	F_1				5	3					
	F_2	3		37	46	15	3	18			
	F_3			39	92	4	10	19	3		
121 (RxR)	F_1			4							
	F_2	7	14	40	30	1	1	2			
	F_3			53	140	1	4				
122 (RxI)	F_1			5	1						
	F_2		9	44	40	4	7	1			
	F_3			38	111	5	2		1		
Total[2]		R = 1,603 (90%)					I = 163 (9%)		S = 14 (1%)		

---

[1] R = resistant; I = intermediate.

[2] Total number of plants classified as resistant, intermediate and susceptible.

in the susceptible class (Table 3). Thus, it would be very easy to select in the F_2 and build up a higher level of resistance in the next generation.

Four crosses -- 237, 238, 240, and 244 -- had more intermediate and susceptible types than the other 8 crosses. Cross number 244 (122 [R/I]//101 [R/I]) in particular accounted for a large percentage of the intermediate (45 percent) and susceptible (71 percent) types. The large number of intermediate and susceptible types of number 244, compared with the reciprocal cross number 234 (101 [R/I]// 122 [R/I]) which had a high percentage of resistance types, could be due to a maternal effect.

III. Intercrossing of Minor Gene Lines (P.I. 178383/Itana// Commercial Wheat Variety), Diallel Cross Number One

Materials and methods. Minor gene lines which were consistent in their reaction type were used for a diallel cross. Head rows of F_6 plants were used as parents for the crosses number 200 through 229. The hybrids and parents were planted, inoculated and read as above. The data were analyzed by the Data Systems Application Division, ARS, USDA, and further analyses of the data to determine gene action, genetic variance, and heritability were done according to Finkner *et al.* (24).

Table 3. Results obtained after intercrossing F_1 plants obtained by intercrossing minor gene lines (P.I. 178383/Itana//Commercial wheat variety).

Cross number	Generation	Number of plants for each infection type									
		Resistant					Intermediate		Susceptible		
		V	00	0-	0	1-	1	2	3+	3	4
233	F_1					3	1				
	F_2			2	20	213			5		
234	F_1				3	1					
	F_2			7	45	140	1	1	6	1	
235	F_1			3	2	1					
	F_2			4	68	149		2	6		
236	F_1			1	3	1	1				
	F_2			7	24	93	2	2	6		
237	F_1				1	1					
	F_2		3	11	23	115	1	4	7	1	
238	F_1			2	1	1	1		1		
	F_2		3	3	14	78	4	6	17	5	
239	F_1					2		1	1		
	F_2		10	30	17	79	3	4	10	3	
240	F_1			1	3	1					
	F_2		12	22	17	101		2	4	3	
241	F_1					1	1				
	F_2		7	37	36	76			4	1	
242	F_1				1	1					
	F_2		4	17	11	123			6		
243	F_1					2	1				
	F_2		2	10	29	92		1	10		
244	F_1				2	2	1				
	F_2			4	9	52	8	16	72	18	17
Total[1]		R = 1,883 (89%)					I = 194 (9%)		S = 49 (2%)		

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[1] Total number of plants classified as resistant, intermediate, and susceptible.

Results and discussion. The weighted means of the parents ranged from 2.1 (infection type, 00) to 5.0 (infection type 1-) -- all resistant (Table 4). All the hybrids were resistant except 2 -- 214 and 222 -- which were intermediate, 6.9 (infection type 2). There was no indication of maternal effects from the mean square of resistant or susceptible types (R or S) or cross products (CP). But significance was shown for the mean square of the infection types (IT) (Table 5A). This was probably due to the more refined classification of plant reaction into 10 types instead of 2. With more refined classifications of reaction type, maternal effects are detected which can be overlooked with a more general classification.

The general combining ability which is an indication of additive gene action was highly significant for IT, R or S, and CP. The specific combining ability which is an indication of non-additive gene action was only significant for the IT. Considering that the general combining ability was significant all through the analysis and its mean square for infection types was 10 times that of the specific combining ability, then the additive genetic effects were more important than non-additive effects. The percentages of additive genetic variance were 91.4 percent (IT), 76 percent

Table 4. Infection types obtained from a diallel cross of minor gene lines (P.I. 178383/Itana/Commercial wheat variety).[1]

Minor gene lines	Infection type[2] 1/ Lancer	1//Rg/Cnn 37-3-6	1/ Delmar	3/ Delmar	2/ Delmar	1/ Lancer
1/Lancer	3.4[3]	4.0	5.4	4.0	5.5	4.4
1//Rg/Cnn 37-3-6	4.0	3.9	4.4	3.6	4.0	5.0
1/Delmar	5.2	4.7	5.0	4.6	5.4	6.9
3/Delmar	4.0	3.3	4.3	2.1	4.3	4.6
2/Delmar	4.6	4.7	6.9	4.2	3.9	5.0
1/Lancer	4.5	5.1	5.5	4.4	5.2	4.8

[1] Diallel analysis of F_1 hybrids and parents.

[2] Infection type ratings 1-10, see page 27.

[3] Infection type of parent.

Table 5. Analysis of the first diallel, intercrossing of minor gene lines (P.I. 178383/Itana//Commercial wheat variety).

A. Mean squares for infection type, resistant or susceptible types and cross products.

Source of Variation	DF	Mean Square Infection type[1]	 Resistant or Susceptible[2]	 Cross Products
General combining ability	5	32.0**[3]	2.6**	9.15**
Specific combining ability	9	3.0**	0.8 N.S.[4]	1.2 N.S.
Maternal	5	0.9**	0.1 N.S.	0.3 N.S.
Reciprocal	10	3.3**	0.5 N.S.	1.1 N.S.
Error	345	0.3	0.7	0.9

[1] Infection type ratings 1 - 10.

[2] Resistant = infection types 1 through 7; susceptible = infection types 8 through 10.

[3] ** - significant at 1% level.

[4] N.S. - non-significant

(R or S), and 88 percent (CP) whereas the percentages of non-additive variance were 8.6 percent (IT), 24 percent (R or S) and 12 percent (CP) (Table 5B). The percentages of broad sense heritability were 99 percent (IT), 83 percent (R or S), and 91 percent (CP). The percentages of narrow sense heritability were 90.6 percent (IT), 63 percent (R or S) and 80.6 percent (CP). Thus, the presence of a high level of additive gene effects and the high heritabilities was a strong indication that the minor-gene resistance can be manipulated in a breeding program.

IV. Intercrossing of Minor Gene Lines (P.I. 178383/Itana//Commercial Wheat Variety) with Commercial Wheats, Diallel Cross Number Two

Materials and methods. Three minor gene lines which were stable for infection type were crossed with 4 susceptible winter wheats: McCall, C.I. 13842; Sundance, C.I. 15327; Trader, C.I. 13998; and Itana, C.I. 12933. The hybrids were numbered from 400 through 441. The hybrids were planted, grown, inoculated, and the data analyzed as previously.

Results and discussion. It was easy to separate the resistant/resistant, the susceptible/susceptible, the resistant/susceptible, and the susceptible/resistant

Table 5 (continued)

B. Gene action and heritabilities of the first diallel.[3]

	Infection type[1]	Resistant or susceptible[2]	Cross products
<u>Mean square:</u>			
Additive: General Combining Ability	32.00	2.65	9.16
Non-Additive: Specific Combining Ability	3.00	0.83	1.24
Experimental Error: Error	0.304	0.71	0.94
Total Genetic Variance (32 + 3)[4]	35.00	3.47	10.40
<u>Analyses of gene action:</u>			
Percentage of additive genetic variance $\left(\frac{32}{35}\right)$	91.4%	76%	88%
Percentage of non-additive genetic variance $\left(\frac{3}{35}\right)$	8.6%	24%	12%
<u>Analyses of heritabilities:</u>			
Percentage of broad sense heritability $\left(\frac{35}{35 + .3}\right)$	99.0%	83%	91.6%
Percentage of narrow sense heritability $\left(\frac{32}{35 + .3}\right)$	90.6%	63%	80.6%

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[1] Infection type ratings 1-10.

[2] Resistant = infection types 1 through 7;
Susceptible = infection types 8 through 10.

[3] Analyses according to Finkner *et al.*(1976)

[4] Shows how numbers for infection type were calculated.

crosses (Table 6). The 3 resistant parents and the 6 resistant/resistant hybrids were highly resistant. The 4 susceptible parents and the 12 susceptible/susceptible crosses were all susceptible. Ten of the resistant/susceptible crosses were intermediate in reaction type and only 2 were susceptible. Seven of the susceptible/resistant crosses were intermediate in reaction type and 5 were susceptible. This would indicate a possible maternal effect where the genetic background of the female would contribute to the expression of resistance. Certain hybrid crosses showed more resistance in the F_1 when the female line was resistant. If the reciprocal crosses -- 1/Lancer//Trader, Trader//1/Lancer -- which were susceptible were removed, there remained 4 susceptible hybrids -- McCall//1/Lancer, Sundance///3//Rg/Cnn, Sundance//1/Lancer, Trader///3//Rg/Cnn -- for the susceptible/resistant crosses and only one -- 1//Rg/Cnn///Sundance -- for the resistant/susceptible crosses.

In general, the intermediate hybrids predominated with 17 out of 24 hybrids intermediate in reaction type. This would be expected for any character of a plant that is controlled by additive gene action; the hybrids are intermediate between the 2 parents. Thus, these data demonstrate

Table 6. Infection types obtained from a diallel cross of minor gene lines (P.I. 178383/Itana//Commercial wheat variety) with susceptible wheats.[1]

	Infection type[2]						
	3//Rg/Cnn 37-3-6	1//Rg/Cnn 37-3-6	1/Lancer	McCall	Sundance	Trader	Itana
	Resistant/Resistant			Resistant/Susceptible			
3//Rg/Cnn	2.5[3] R[4]	3.0 R	3.1 R	7.0 I	7.1 I	5.8 I	7.2 I
1//Rg/Cnn	2.8 R	2.9 R	4.2 R	7.1 I	7.8 S	7.0 I	7.0 I
1/Lancer	2.5 R	3.8 R	3.0 R	7.4 I	6.9 I	8.6 S	7.3 I
	Susceptible/Resistant			Susceptible/Susceptible			
McCall	7.1 I	7.4 I	8.9 S	8.7 S	9.0 S	8.9 S	8.8 S
Sundance	7.5 S	5.8 I	7.7 S	9.0 S	8.0 S	8.7 S	8.9 S
Trader	7.5 S	7.0 I	7.8 S	9.0 S	8.9 S	8.3 S	8.9 S
Itana	6.5 I	6.6 I	7.1 I	9.1 S	9.0 S	8.9 S	7.7 S

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[1] Diallel analysis of F_1 hybrids and parents.
[2] Infection type ratings 1 through 10, see p. 27.
[3] Infection type of parent.
[4] R = resistant, I = intermediate, S = susceptible.

the presence of an additive resistance in the minor gene lines.

V. Intercrossing of Winter Wheats and Selection on Progeny

Introduction. Because of the possibility of finding minor genes in normally susceptible wheats, commercially acceptable winter wheats were intercrossed and their progeny evaluated for stripe rust resistance. The use of commercial cultivars as parents would reduce the undesirable traits usually associated with various plant introductions.

Materials and methods. The 10 winter wheats used in these studies were: Itana, C.I. 12933; Lancer, C.I. 13547; Delmar, C.I. 13442; McCall, C.I. 13842; Wanser, C.I. 13844; Teton, C.I. 15244; Cheyenne, C.I. 8885; Centurk, C.I. 15075; Winalta, C.I. 13670; and a Montana line, MT 7015. These varieties are all good agronomic types and, with the exception of MT 7015, are grown commercially. All these varieties lack specific resistance to stripe rust and vary from intermediate to susceptible in their reaction to stripe rust (Table 7). Forty-one hybrids were made by intercrossing these varieties in the summer of 1973. These crosses were numbered from 15 to 55. The hybrids and

Table 7. Disease reactions to stripe rust of parental wheat plants in the seedling and mature plant stages.

Wheat Cultivar			Disease Ratings	
			Seedling	Field
Winter wheats:				
Cultivar	Abb.	C.I. number		
Itana	IT	C.I. 12933	S[1]	S
Lancer	LCR	C.I. 13547	I	I
Delmar	DM	C.I. 13442	I	I
McCall	MC	C.I. 13842	S	S
Wanser	WSR	C.I. 13844	S	I
Teton	TN	C.I. 15244	I	I
Cheyenne	CNN	C.I. 8885	I	I-S
Centurk	CNTK	C.I. 15075	I	I-S
Winalta	WN	C.I. 13670	S	I
MT 7015			S	I
Spring wheats:				
Shortana	SRT	C.I. 15233	S	I
World Seeds	WS1809	C.I. 15012	R	
Centana	CNT	C.I. 12974	S	I
World Seeds	WS1812	C.I. 14585	R	
Wells	WLS	C.I. 13333	S	I
Leeds	LDS	C.I. 13768	S	I
Bonanza	BNN	C.I. 14077	R	
Fortuna	FTA	C.I. 13596	R	I-R
Manitou	MIT	C.I. 13775	I	I
Sheridan	SI	C.I. 13586	I	
Thatcher	TC	C.I. 10003	I	I
Polk		C.I. 13773	R	

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[1] R = resistant; I = intermediate; S = susceptible.

their parents were evaluated for infection type in the fall of 1973 under the standard conditions. Starting with the F_2 generation, each segregating generation was also evaluated under standard conditions. The most resistant progeny of each generation (10 to 20 percent) were selected, transplanted and grown to produce seed for the next generation. This procedure was continued for 4 generations of selection. Three crosses -- 19, 20, and 45 -- were dropped from the program because of a lack of F_2 seed production.

Results and discussion. All F_1 hybrids and F_2 progeny from 33 of the 38 crosses were susceptible in seedling tests (Table 8). An average of 171 F_2 plants were read for each cross. From a total of 6,172 plants, none were resistant, 8 (0.12 percent) were intermediate, and 6,164 (99.88 percent) were susceptible (Table 8). Intermediate reaction types were expressed only in the F_2 of 5 crosses -- 30, 46, 47, 48 and 49. Teton, an intermediate resistant variety, was the female parent in 4 of these crosses and male parent in the other cross. Thus, the intermediate resistance of Teton has been a source of greater resistance than the other susceptible lines.

Table 8. Transgressive segregation for stripe rust resistance after selection and selfing of segregating populations of winter wheat.

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
15							P_1				
Cheyenne/Centurk						P_2					
									F_1		
F_2								16	134		150
F_3							1	10	155		166
F_4				1	4	8	16	118	19		165
F_5				37	43	44	85				209
16							P_1				
Cheyenne/Delmar							P_2				
									F_1		
F_2								16	150	2	168
F_3							18	40	115	21	194
F_4					3	6	63	46	22		140
F_5				44	17	32	32	8			133
17							P_1				
Cheyenne/Itana									P_2		
									F_1		
F_2								6	122		128
F_3								12	90		102
F_4						4	6	96	64	6	176
F_5				2	1	17	156	22			198

Table 8 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
18							P_1				
Cheyenne/Lancer							P_2		F_1		
F_2								19	210	19	248
F_3							18	10	155	12	195
F_4						4	51	98	68		221
F_5				4	7	28	142	4			185
21						P_1			P_2		
Centurk/Itana									F_1		
F_2								17	240	13	270
F_3							4	7	130	25	166
F_4							1	28	138	1	168
F_5				1	3	3	134	29	3		173
22						P_1	P_2				
Centurk/Lancer									F_1		
F_2								15	214	18	247
F_3								8	60		68
F_4				12	16	25	68	51	4		176
F_5				89	37	51	35				212
23						P_1			P_2		
Centurk/MT 7015									F_1		
F_2								18	126	3	147
F_3							14	12	120	12	158

Table 8 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
24						P_2	P_1				
Delmar/Centurk									F_1		
F_2								9	141		150
F_3							1	11	115		127
F_4						6	32	65	45		148
F_5				9	6	23	132	9	1		180
25							P_1		P_2		
Delmar/McCall									F_1		
F_2								10	112	5	127
F_3								20	160	12	192
F_4						3	20	83	45	5	156
F_5						2	65	45	19		131
26							P_1				
Delmar/MT 7015							P_2		F_1		
F_2								16	139		155
F_3								20	160	12	192
F_4					5	4	14	64	73	6	166
F_5				17	3	11	88	21			140
27							P_1				
Delmar/Teton							P_2		F_1		
F_2								21	53		74
F_3							10	30	95		135
F_4				16	15	14	17	22			84
F_5			1	125	15	16	13	1			171

Table 8 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
28							P_1	P_2			
Delmar/Winalta									F_1		
F_2								12	114	1	127
F_3					1	1	21	77	43	6	149
F_4				2	1	45	50	38			136
29							P_2		P_1		
Itana/Delmar									F_1		
F_2								5	183	6	194
F_3								12	107	17	136
F_4							7	72	97	6	182
F_5						1	19	65	47		132
30						P_2			P_1		
Itana/Teton									F_1		
F_2							2	13	119	60	194
F_3							17	57	142		216
F_4				30	42	26	24	21	3	1	147
F_5				9	14	35	80	2			140
31								P_2	P_1		
Itana/Wanser									F_1		
F_2								10	200	2	212
F_3							13	43	130	12	198
F_4				2	5	22	52	38	19	4	142
F_5				32	11	11	112	5			171

Table 8 (continued)

Identification of crosses	Number of plants for each infection type										Total
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	
32							P_1				
Lancer/Delmar							P_2		F_1		
F_2								7	130	60	197
F_3							8	80	50		138
F_4						5	37	64	7		113
F_5				1	2	10	96	16	6		131
33							P_1		P_2		
Lancer/Itana									F_1		
F_2								15	260		275
F_3								11	152	50	213
F_4								9	139	4	152
F_5				1	2	8	192	32	3		238
34							P_1		P_2		
Lancer/McCall									F_1		
F_2								5	140		145
F_3								11	131	30	172
F_4					3	15	52	61	30	5	166
F_5				35	6	2	57	13			113
35							P_1	P_2			
Lancer/Wanser									F_1		
F_2								16	150	19	185
F_3								17	130	5	152
F_4								40	122	2	164
F_5				9	11	23	131	5	4		183

Table 8 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
36 McCall/Centurk						P_2			P_1 F_1		
F_2								2	191		193
F_3								10	120	22	152
F_4							9	26	129	12	176
F_5				3	7	16	138	5	1		170
37 McCall/Itana									P_1 P_2 F_1		
F_2								8	240		248
F_3								5	110	57	172
F_4							3	16	139	10	168
F_5						6	132	60	11		209
38 McCall/MT 7015									P_1 P_2 F_1		
F_2								11	161	23	195
F_3								15	110	7	132
F_4							1	34	164	1	200
F_5				15	8	39	138	3			203
39 McCall/Wanser								P_2	P_1 F_1		
F_2								7	211		218
F_3								7	167		174
F_4							1	4	147		152

Table 8 (continued)

Identification of crosses	Number of plants for each infection type Resistant V	 00	 0-	 0	 1-	 Intermediate 1	 2	 Susceptible 3-	 3	 4	Total
40							P_2		P_1		
MT 7015/Cheyenne									F_1		
F_2								13	159	20	192
F_3							17	20	100	36	173
F_4				7	19	23	54	9	2		114
F_5		1	17	151	3	1	13				186
41									P_1		
MT 7015/Itana									P_2 F_1		
F_2								21	235		256
F_3								10	175	30	215
F_4								7	107	1	115
F_5					2	11	147	45	7		212
42							P_2		P_1		
MT 7015/Lancer									F_1		
F_2								26	122	4	152
F_3							18	6	122	8	154
F_4					5	3	40	25	60		133
F_5		1	21	142	10	5	12		1		192
43								P_2	P_1		
MT 7015/Wanser									F_1		
F_2		(No selection at F_2)									
F_3								12	112	50	174
F_4							1	50	92	5	148
F_5						1	76	74	27		178

Table 8 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
44								P_2	P_1		
MT 7015/Wanser									F_1		
F_2	(No selection in F_2)										
F_3								13	122	21	156
F_4							9	86	30	11	136
F_5					1	2	97	35	10		145
46						P_1	P_2				
Teton/Delmar									F_1		
F_2	(No selection in F_2)										
F_3				8	10	3	47	108	31		207
F_4				95	17	19	9	3			143
F_5			5	121	3	2	1				132
47						P_1	P_2				
Teton/Lancer									F_1		
F_2	(No selection in F_2)										
F_3				3		2	36	88	51		180
F_4				15	21	13	25	5			79
F_5			5	151	29	24	9				218
48						P_1			P_2		
Teton/McCall									F_1		
F_2							2	19	105		126
F_3				1	4	5	60	100	25		195
F_4				20	35	18	53	6	1		133

Table 8 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant				Intermediate			Resistant			
	V	00	0-	0	1-	1	2	3-	3	4	Total
49						P_1			P_2		
Teton/MT 7015									F_1		
F_2							4	19	107		130
F_3			1	1		1	32	69	49	4	157
F_4				53	20	28	30	4	4		139
50						P_2		P_1			
Wanser/Centurk									F_1		
F_2								15	105	3	123
F_3								34	110	16	160
F_4							7	56	40	2	105
F_5				4	10	10	127	34	4		189
51							P_2	P_1			
Wanser/Delmar									F_1		
F_2								17	90	21	128
F_3								12	110	15	137
F_4						1	28	97	40		166
52						P_2		P_1			
Wanser/Teton									F_1		
F_2								16	138		154
F_3					1	3	32	100	40		176
F_4				40	33	41	56	2			172

Table 8 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
53							P_2	P_1			
Winalta/Cheyenne									F_1		
F_2									150		150
F_3				1			1	15	125	6	148
F_4		4	46	78	24	18	2		13		185
54						P_2		P_1			
Wanalta/Centurk									F_1		
F_2								2	93	10	105
F_3								5	145	55	205
F_4						1	18	60	89		168
55								P_1	P_2		
Winalta/McCall									F_1		
F_2									75		75
F_3								5	144	33	182
F_4			15	60	40	55	3	5			178

An average of 166 F_3 plants were read for each cross. From a total of 6,301 plants, 31 (0.5 percent) were resistant, 393 (6.2 percent) were intermediate, and 5,877 (93.3 percent) were susceptible (Table 8). Nineteen crosses had no F_3 progeny with intermediate infection types and 19 crosses had progeny with intermediate infection types (Table 8). Five crosses involving Teton as a parent -- 46, 47, 48, 49 and 52 -- had at least one F_3 plant with a resistant infection type. One other cross, 53, had one F_3 individual which was resistant.

From a total of 5,575 plants in the F_4 segregating populations, 804 (14 percent) were resistant, 1,274 (23 percent) were intermediate and 3,497 (63 percent) were susceptible. Progeny from 35 crosses were classified as having intermediate infection types (Table 8). The lack of intermediate types in 3 crosses -- 33, 35 and 41 -- was probably due to sampling error of the population or experimental error in reading the populations because of the resistance found in the following F_5 generation of these crosses. Resistant F_4 progeny were found in 18 of the crosses (47 percent).

In the F_5 generation all crosses had progeny with intermediate levels of resistance (Table 8). From a total of 4,696 plants, 1,304 (28 percent) were resistant, 2,816 (60 percent) were intermediate, and 576 (12 percent) were susceptible. Twenty-four crosses out of 27 crosses for which datawere available for the F_5 generation have at least one resistant plant. Thus, in the F_5 generation, 89 percent of the crosses produced resistant progeny where only susceptible types were present in the early generations.

In general, the methods used to accumulate stripe rust resistance were effective in all 38 crosses. Resistant plants increased from 0.5 percent in the F_3, to 14 percent in the F_4, and to 28 percent in the F_5 generation. Intermediate plants increased from 0.12 percent in the F_2, to 6.2 percent in the F_3, to 23 percent in the F_4, and to 60 percent in the F_5 generation. Susceptible plants decreased from 100 percent in the F_1, to 99.8 percent in the F_2, to 93.3 percent in the F_3, to 63 percent in the F_4, and to 12 percent in the F_5 generation. Resistance was developed earlier in some crosses than others; but by the F_4 generation, all crosses showed transgressive segregation for intermediate or moderate resistance above the parents and F_1 hybrids. By the F_5, 89 percent of the crosses had progeny with even higher levels of resistance. It should be possible to further shift the distribution toward a higher level of resistance with continued selection and selfing.

VI. Field Evaluation of F_2 and F_3 Generations of the Winter Wheat Crosses

Materials and methods. Field studies were undertaken to determine if the same methods were applicable when observations were made of adult plants rather than of seedlings. The F_1 hybrids for 28 crosses were grown in the field for F_2 seed production. Twenty-seven F_2 populations were planted as described in the general materials and methods. At the 10.5 stage of growth (48) when the plants were at the right stage for reading, each individual plant in each F_2 population was read for stripe rust as described in the general materials and methods. The most resistant plants were saved and bulked for the F_3 generation. In 1975, a few plants in 8 populations -- 21, 22, 24, 25, 31, 32, 42, and 46 -- were tagged as being more resistant than most of the selected plants. These few plants were bulked for each population and planted separately for the F_3 generation. For example, cross number 21 had 2 F_3 populations to evaluate the following year.

In 1976, 35 segregating populations were read. The most resistant plants were saved and harvested individually for evaluation in plant rows in 1977, an average of 11 plants (12 percent) per population. The data for the F_2 and F_3 generations were tabulated so that the difference between the generations could be observed. An estimate of the "general combining ability" of the parents was calculated by taking the average of the percentage of the intermediate types for all crosses involved with an individual parent. This estimate is not very accurate because of the variation in the number of crosses for each parent and an imbalance due to number of times a parent was used as a female or male.

Results and discussion. An average of 100 individual plants (range 72-151) were read for each of 27 F_2 populations. From a total of 2,686 plants, 2,138 (80.7 percent) were susceptible, 534 (19.9 percent) were intermediate, and 14 (0.5 percent) were resistant (Table 9). Only 6 of 27 crosses had resistant plants. Delmar was involved in the parentage of 4 of these crosses -- 16, 24, 25, and 32.

Table 9. Results of field observations of F_2 and F_3 populations of winter wheat crosses.

Cross number	Disease ratings						
	Number of plants[1]			Cross number	Number of plants[2]		
	R[3]	I	S		R	I	S
16-2 CNN/DM[4]	2	24	53	16-3	3	17	70
17-2 CNN/IT	0	0	79	17-3	0	0	82
21-2 CNTK/IT	0	4	96	21-3	1	17	76
				21-3I	1	24	63
22-2 CNTK/LCR	3	24	88	22-3	8	42	47
				22-3R	10	55	29
24-2 DM/CNTK	5	23	74	24-3	1	37	62
				24-3R	1	55	47
25-2 DM/MC	2	12	73	25-3	0	16	61
				23-3R	1	35	58
26-2 DM/MT 7015	0	28	71	26-3	0	6	76
28-2 DM/WN	0	33	85	28-3	2	17	70
29-2 IT/DM	0	19	62	29-3	0	7	93
30-2 IT/TN	0	16	81	30-3	0	9	88
31-2 IT/WSR	0	12	103	31-3	0	1	76
				32-3I	2	22	60
32-2 LCR/DM	1	53	44	32-3	2	43	37
				32-3I	3	57	11
33-2 LCR/IT	0	3	148	33-3	0	11	67
34-2 LCR/MC	0	6	66	34-3	5	46	38
37-2 MC/IT	0	2	103	37-3	0	69	20
38-2 MC/MT 7015	0	10	66	38-3	0	27	33

Table 9 (continued)

		Disease ratings						
	Cross number	Number of plants[1]			Cross number	Number of plants[2]		
		R[3]	I	S		R	I	S
39-2	MC/WSR	0	12	99	39-3	0	74	10
40-2	MT 7015/CNN	0	6	103	40-3	0	62	29
41-2	MT 7015/IT	0	2	93	41-3	5	77	15
42-2	MT 7015/LCR	1	19	91	42-3	0	76	8
					42-3R	5	82	0
46-2	TN/DM	0	56	39	46-3	7	53	7
					46-3R	22	84	0
48-2	TN/MC	0	59	56	48-3	0	94	4
49-2	TN/MT 7015	0	48	61	49-3	4	74	6
50-2	WSR/CNTK	0	38	65	50-3	35	55	7
51-2	WSR/DM	0	8	81	51-3	4	70	11
53-2	WSR/CNN	0	1	83	53-3	2	97	16
54-2	WN/CNTK	0	16	75	54-3	3	77	12
	Total	14	534	2,138		127	1,588	1,389
	Percent	0.5	19.9	80.7		4	51.2	44.7

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[1] 1975 F_2 plants.

[2] 1976 F_3 plants.

[3] R = resistant; I = intermediate; S = susceptible.

[4] Abbreviations are listed in Table 8.

An average of 89 individual plants (range 60-115) were read for stripe rust for each of 35 F_3 populations. A total of 3,104 plants were read: 1,389 (44.7 percent) susceptible, 1,588 (51.2 percent) intermediate, and 127 (4 percent) resistant (Table 9). Twenty-two populations out of 35 (63 percent) had resistant plants. Delmar was involved in parentage of 11 (50 percent) of those crosses.

The selection in the F_2 population, mainly for intermediate resistance types, was effective in shifting the F_3 population to a higher level of resistance (Table 9). The number of susceptible plants in the population was reduced from 2,138 (80.7 percent) to 1,389 (44.7 percent) in 1976. The number of plants with the intermediate reaction type was increased from 534 (19.9 percent) in 1975 to 1,588 (51.2 percent) in 1976. The number of resistant plants was increased from 14 (0.5 percent) to 127 (4 percent) in 1976.

Considering the F_3 data from the 8 crosses -- 21, 22, 24, 25, 31, 32, 42, and 46 -- which had 2 populations, one of which had been from the most resistant plants of the selected plants and one which included the regular selected plants, there was additional progress made. With regular selection of the 8 populations, 55 percent of the plants were susceptible versus 37 percent with extra selection. The number of intermediate types was 42 percent versus 57 percent of the population and numbers of resistant types were 3 percent versus 6 percent of the populations. Thus, if a few plants are selected in the F_2 with the highest level of resistance and the genetic base of the population is narrowed, faster progress can be made.

It can be concluded that good resistance was developed even with one selection in the segregating populations. It is assumed that even more progress would have been made if the F_2 could be compared with the F_4 populations.

The best 10 crosses based on the percentage of F_2 plants in the intermediate and resistant classes in 1975 were: number 46, Teton/Delmar (59 percent); number 32, Lancer/Delmar (55 percent); number 48, Teton/McCall (51 percent); number 49, Teton/MT 7015 (44 percent); number 50, Wanser/Centurk (37 percent); number 16, Cheyenne/Delmar (33 percent); number 26, Delmar/Winalta (28 percent); number 28, Delmar/Winalta (28 percent); number 24, Delmar/Centurk (23 percent); and number 29, Itana/Delmar (23 percent). Delmar was involved in the parentage of 7 of the 10 crosses. Teton was next by being in the parentage of 3 of the top 5 lines.

The best 10 crosses based on the percentage of F_3 plants in the intermediate and resistant classes in 1976 were: number 42-3R, MT 7015/Lancer (100 percent); number 46-3R, Teton/Delmar (100 percent); number 48-3, Teton/McCall (96 percent); number 49-3, Teton/MT 7015 (93 percent); number 50-3, Wanser/Centurk (93 percent); number 42-3, MT 7015/Lancer (90 percent); number 46-3, Teton/Delmar (89 percent); number 39-3, McCall/Wanser (88 percent); number 51-3, Wanser/Delmar (87 percent); and number 54-3, Winalta/Centurk (87 percent).

When the F_2 and F_3 rankings were compared, Teton stood out as a good source of resistance. It was the female parent in the crosses ranked 1, 3, and 4 in 1975 and in the crosses ranked 2, 3, and 4 in 1976. In 1976, Teton was rated as intermediate in the field as were several other parents. The good performance of 3 crosses with Teton could be due to additive gene action or a dominant gene action involved in the expression of resistance in its progeny.

The results of the crude estimate of "general combining ability" for each parent are presented in Table 10. Teton was rather consistent by being number 1 in 1975 and

Table 10. Ranking of parents as sources of stripe rust resistance according to an estimate of "general combining ability".

		1975		1976		1976	
Varieties	Number Crosses[1]	Rank	Average % I[2]	Rank	Average % I[2]	Rank	Average % I & R[2]
Winters:							
Teton	3	1	42.5	4	61.3	2	64.6
Delmar	9	2	27.6	9	35.9	9	38.2
Winalta	2	3	23.0	5	51.5	6	54.0
Centurk	5	4	20.6	7	47.8	5	57.6
Lancer	5	5	20.4	6	50.2	7	53.2
MT 7015	6	6	18.3	2	62.8	3	64.5
McCall	6	7	16.5	1	63.3	4	64.1
Wanser	5	8	13.6	3	62.4	1	71.0
Cheyenne	4	9	9.3	8	42.8	8	44.1
Itana	8	10	7.4	10	25.8	10	26.6

Table 10 (continued)

		1975	
Varieties	Number Crosses[1]	Rank	Average % I[2]
Springs:			
WS1809	3	1	66.6
Bonanza	9	2	57.4
Manitou	7	3	43.7
Thatcher	5	4	34.0
Polk	4	5	33.7
WS1812	4	6	31.7
Sheridan	5	7	31.6
Shortana	7	8	31.6
Fortuna	5	9	25.4
Centana	9	10	20.1

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[1] Number of crosses the cultivar was used as a parent.

[2] I = intermediate; R = resistant.

number 2 in 1976. Cheyenne and Itana were consistent by staying on the bottom of the list. The intermediate varieties -- Winalta, Centurk, Lancer, MT 7015, and McCall -- shifted slightly. But the big differences between the F_2 and F_3 were with Delmar and Wanser. Delmar went from number 2 in F_2's to number 9 in the rankings in F_3's, and Wanser went from number 8 in F_2's to number 1 in F_3's. The reason for the change in rankings is rather unclear for Delmar although it is consistent with the drop in the number of top ranked crosses having Delmar in their parentage. Perhaps the resistance in the F_2 was due to non-additive effects which did not carry over to the F_3 progeny or environmental differences. Only one cross with Wanser in its parentage was in the top ranked crosses in F_2's; but in F_3's, 3 of the 5 Wanser crosses were among the best crosses. Perhaps this was due to a breaking up of linkage groups by the selfing of the F_2 plants which allowed more additive combinations for expression of resistance in the F_3. MT 7015 was ranked 3 in the F_3's and was also found in the parentage of 3 of the top ranked crosses. Thus, the "general combining ability" gives a rough estimate of the ability of a variety to express resistance in combination with other varieties.

VII. Intercrossing of Spring Wheats with Different Levels of Seedling Resistance

Materials and methods. Ten commercial varieties of common spring wheat were intercrossed in the summer of 1973 to give 43 crosses numbered 56 through 98. The varieties used were: Bonanza, C.I. 14077; Centana, C.I. 12974; Fortuna, C.I. 13596; Manitou, C.I. 13775; Polk, C.I. 13773; Sheridan, C.I. 13586; Shortana, C.I. 15233; Thatcher, C.I. 10003; World Seeds 1809, C.I. 15012; and World Seeds 1812, C.I. 14585. Two durum wheats, *Triticum durum,* Leeds, C.I. 13768; and Wells, C.I. 13333, were intercrossed to form 2 crosses numbered 99 and 100.

The parents and the hybrids were screened for stripe rust resistance in the fall of 1973 under standard conditions. Starting with the F_2 generation, each segregating population was also evaluated for stripe rust resistance. The most resistant progeny of each generation (10 to 20 percent) were selected, transplanted and grown to maturity for seed production for the next generation. This continued for 4 generations. The populations which were nearly or completely resistant in the F_5 generation were subjected to a total of 5 different races: B-1, tentative race number 3 by Volin; BF-Mo, tentative race number 4, Cv1-C166, tentative race number 8, Ms1-We, tentative race number 10; and Pn-C166, tentative race number 11 (117).

Results and discussion. The spring wheat parents were classified as resistant (Bonanza, Fortuna, Polk, World Seeds 1809, World Seeds 1812), intermediate (Manitou, Thatcher, Sheridan), and susceptible (Centana, Shortana) (Table 11). From a total of 5,938 F_2 plants, 3,324 (55.9 percent) were susceptible, 1,739 (29.3 percent) were intermediate, and 875 (14.7 percent) were resistant (Table 12). Only 13 crosses out of 43 -- 64, 74, 76, 77, 78, 79, 82, 86, 87, 88, 89, 92, and 94 -- did not have resistant plants in their F_2 populations (Table 12).

There was an increase in the percentage of resistant plants in the F_3 populations. From a total of 3,340 F_3 plants, 959 (28.7 percent) were resistant, 959 (28.7 percent) were intermediate and 1,422 (42.6 percent) were susceptible (Table 12). Only 12 crosses -- 74, 77, 79, 80, 81, 82, 87, 88, 89, 90, 92, and 94 -- did not have resistant plants in the F_3 populations (Table 11). Considering both F_2 and F_3 populations, there were 9 crosses -- 74, 77, 79, 82, 87, 88 89, 92, and 94 -- which did not have resistant plants in either filial generation.

Table 11. Transgressive segregation for stripe rust resistance after selection and selfing of segregating populations of commercial spring wheats.

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
56				P_1				P_2			
Bonanza/Centana								F_1			
F_2	1	11	26	11	3	1	15	38	78		184
F_3	3	7	9	15	3	6	17	2	7		69
F_4	1	18	11	2				2			34
F_5	1	32	26	48							107
F_6		72	70	18							160
57				P_1			P_2				
Bonanza/Manitou							F_1				
F_2	2	15	23	14	6	8	58	52	25		203
F_3	1	3	15	40	3	6	57		1		126
F_4	19	44	20	3							86
F_5		7	31	102							140
F_6 (5 races)	22	39	58	49							168
58				P_1							
Bonanza/Polk				P_2				F_1			
F_2		7	23	32	1	6	24	25	45		163
F_3		10	3	15	1	1					30
F_4	6	30	10	23	1	3	27				100
F_5	9	37	42	71	3						162
F_6 (5 races)	14	45	36	31	2						128

Table 11 (continued)

Identification of crosses	Number of plants for each infection type										Total
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	
59				P_1			P_2				
Bonanza/Sheridan			F_1								
F_2		11	3	8	18	15	22	16	15		108
F_3		8	11	40	7	4	12	9	3		94
F_4		2	38	97	11	38	12				198
F_5	13	48	69	30							160
60			P_1			P_2					
Bonanza/Thatcher						F_1					
F_2		4	8	8	3	4	63	15			105
F_3		2	10	18							30
F_4			2	42	12	22	68	52	11		209
F_5			19	163	10						192
F_6 (5 races)	51	52	23	27							153
61				P_1							
Bonanza/WS1809				P_2		F_1					
F_2		4	7	25		1	41	3			81
F_3		12	6	11							29
F_4	4	18	19	45	1	1	5				93
F_5	89	70	12	4							175
F_6 (5 races)	1	8	26	69	1						105

Table 11 (continued)

Identification of crosses	Number of plants for each infection type										Total
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	
62 Bonanza/WS1812		P_2 F_1		P_1							
F_2	22	22	14	12			11				81
F_3		10	11	22	1		3				47
F_4	23	44	16	12		1	3	1			100
F_5	20	100	47	12	2						181
F_6 (5 races)	2	39	30	60	1	1	2				135
63 Centana/Bonanza				P_2				P_1 F_1			
F_2		1	20	27	6	5	60	55	33		207
F_3		4	20	81	23	19	15	8	1		171
F_4			19	98	4	2					123
F_5		2	23	129	9	19	20				202
64 Centana/Polk				P_2				P_1	F_1		
F_2						2	35	79	47		163
F_3				28	16	18	59	33	10		164
F_4			29	77	2						108
F_5			3	63	12	19	47	6			150
65 Centana/WS1809				P_2				P_1 F_1			
F_2				2	1		12	62	115		192
F_3			3	8	1	1	60	30	13		116
F_4				5	3	3	50	15	1		77
F_5				77	20	9					106
F_6				53	20	20	6				99

Table 11 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant				Intermediate			Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
66		P_2						P_1			
Centana/WS1812							F_1				
F_2		6	7	3	2	1	10	45	65		139
F_3	3	27	22	19	4	2	21	28	29	1	156
F_4	9	67	28	16	1		6	2			129
F_5	26	42	13	10	1						92
67				P_2	P_1						
Fortuna/Bonanza			F_1								
F_2		11	20	24	8	8	34	27	13		145
F_3	15	32	17	15		4	16	3			102
F_4	3	20	12	18	4	3	18	6	2		86
F_5	10	39	108	1							158
F_6 (5 races)		6	31	145	1	2	2				187
68					P_1			P_2			
Fortuna/Centana								F_1			
F_2				1	5	11	50	67	30		164
F_3	7	13	3	6		2	10	15	3		59
F_4		5	7	7	6	13	100	3			141
F_5				6	14	11	23	17	2		73
F_6	1	5	18	140	1	1					166
69					P_1		P_2				
Fortuna/Manitou			F_1								
F_2			15	47	26	14	31	29	3		165
F_3	1	3	7	3	1	2	8	6			31
F_4	2	15	13	36		4	52	6	4		132
F_5		1	130	10	6						147
F_6 (5 races)		4	24	72	11	14	7				132

Table 11 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant				Intermediate			Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
70				P_2	P_1						
Fortuna/Polk								F_1			
F_2	1	1	1	7	1	2	28	15	5	1	62
F_3		(No selection in F_3)									
F_4	1	5	3	15		2	55	17	11		109
F_5		5	16	33	4	21	29	6	9		123
F_6		3	65	192							260
71					P_1		P_2				
Fortuna/Sheridan								F_1			
F_2			3	15	6	15	64	17	14		134
F_3		1	2	8		6	45	15	1		78
F_4		2	9	12	1	3	10	5	9		51
F_5			4	63	38	11	7				123
F_6 (5 races)			2	20	14	15	69	1			121
72					P_1			P_2			
Fortuna/Shortana								F_1			
F_2			1	5	15	21	69	32	21		164
F_3	4	6	3	4	1	1	36	9	31		95
F_4		1	1	3	6	10	92	20	3		136
F_5			5	50	19	23	15				112
F_6		6	20	121		1	8				156
73		P_2			P_1						
Fortuna/WS1812						F_1					
F_2	7	5	10	2	9	3	27	7	4		79
F_3		1	2	9	5		10	3	1		31
F_4	9	29	11	9		1	18	19	4		100
F_5	7	75	32	26	3		13				156
F_6 (5 races)	8	66	14	40	1		1				130

Table 11 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
74							P_1	P_2			
Manitou/Centana								F_1			
F_2							11	48	37		96
F_3							3	10	10		23
F_4				2	4	8	32	46	75	4	171
F_5						22	39	57	23		141
F_6			8	148	8	9	4				177
75				P_2			P_1				
Manitou/Polk								F_1			
F_2				3	1	1	18	39	19		81
F_3				2	2	1	30	3	2		40
F_4				7	6	8	52	42	25		140
F_5				45	24	26	54	16	1		166
F_6				92	14	10	3				119
76							P_1	P_2			
Manitou/Shortana									F_1		
F_2						5	14	25	71		115
F_3				1	1		15	138	85		240
F_4					3	7	55	101	20		186
F_5			7	80		2	2				91
77						P_2	P_1				
Manitou/Thatcher							F_1				
F_2						1	84	9			94
F_3							31	64	31		126
F_4					1	9	42	77	50		179
F_5				1		3	97	64	8		173
F_6				37	31	42	48				158

Table 11 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
78				P_1				P_2			
Polk/Shortana										F_1	
F_2						2	5	40	80		127
F_3				1			4	25	88	1	119
F_4		(No selection in F_4)									
F_5				25	6	4	44	36	21		136
79							P_1	P_2			
Sheridan/Centana										F_1	
F_2							28	66	50	5	149
F_3								4	105	30	139
F_4							1	51	81	1	134
F_5							4	47	129	9	189
F_6				62	10	19	56	4	1		152
80							P_1				
Sheridan/Manitou							P_2	F_1			
F_2				9	4	8	59	73	55		208
F_3						10	45	50	30		135
F_4				13	9	15	61	37	15		150
F_5			1	40	4	11	24	3			83
F_6		14	35	160	1		1				211
81				P_2			P_1				
Sheridan/Polk									F_1		
F_2	2	3	6				15	9	21	3	59
F_3		(No selection in F_3)									
F_4	8	33	16	11	3	1	10	36	37	3	158
F_5		35	38	27	1	1	6	10			118
F_6	13	75	102	36							226

Table 11 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
82						P_2	P_1				
Sheridan/Thatcher									F_1		
F_2								5	145	15	165
F_3								10	107	11	128
F_4							2	17	46	5	70
F_5				8	2	26	136	87	28	1	288
F_6				2	3	8	74	17			104
83				P_2			P_1				
Sheridan/WS1809								F_1			
F_2				1			12	32	55	4	104
F_3			2	37	3	10	30	12			94
F_4			7	95	2	3	10				117
84		P_2					P_1				
Sheridan/WS1812							F_1				
F_2		13	9	3	1	2	55	41	12		136
F_3		5	2	2			9	3	1		22
F_4	102	33	9	5	1	5	1				156
F_5		101	55	23	1						180
F_6 (5 races)	13	66	53	24							156
85				P_2				P_1			
Shortana/Bonanza								F_1			
F_2		5	6	3		5	45	60	50		174
F_3	8	37	31	33	6	8	48	11	2		184
F_4		21	22	62	6	8			2		121
F_5	8	71	51	21							151

Table 11 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
86								P_1			
Shortana/Centana								P_2		F_1	
F_2								2	143	27	172
F_3				1		1		5	45	5	57
F_4		5	4	21	2		8	21	85	21	167
F_5		7	59	246	15	7	4				338
F_6		12	20	53			1				86
87						P_2		P_1			
Shortana/Thatcher								F_1			
F_2							1	29	137		167
F_3		(No selection in F_3)									
F_4							53	163	81	3	300
88				P_2				P_1			
Shortana/WS1809								F_1			
F_2							14	27	81	31	153
F_3							6		25		31
F_4			1		3	4	108	101	28		245
89						P_1		P_2			
Thatcher/Centana									F_1		
F_2							16	47	58	10	131
F_3								30	40		70
F_4						2	17	41	34	1	95
F_5				1	1	21	86	41	2		152
F_6				10	4	9	37				60

Table 11 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
90					P_2	P_1					
Thatcher/Fortuna							F_1				
F_2			1	10	3		32	63	28	1	138
F_3						3	12	10	10		35
F_4		5	21	64	17	10	47				164
F_5			4	78	23	13	35	6			159
F_6			12	77							89
91				P_2		P_1					
Thatcher/Polk							F_1				
F_2				4	1	4	72	61	24		166
F_3		2		1			40	20	10		73
F_4		2	3	12	5	9	57	7			95
F_5		1	9	112	5	3	22	1			153
F_6		6	38	54		1	2				101
92						P_1	P_2				
Thatcher/Sheridan									F_1		
F_2							23	70	41	9	143
F_3							1	10	5		16
F_4			1	1	11	22	90	47	32		204
F_5			17	53	14	6	21	3	1		115
F_6		1	20	44	1	2					68
93				P_1	P_2						
WS1809/Fortuna							F_1				
F_2			1	9	8	7	90	44	12		171
F_3				2		4	5	15			26
F_4		2	7	6	37	6	81	5			144
F_5			1	24	5	5	49	63	4		151
F_6	4	23	59	55							141

Table 11 (continued)

Identification of crosses	Number of plants for each infection type										
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	Total
94				P_1			P_2				
WS1809/Manitou							F_1				
F_2						1	92	9			102
F_3						5	140	25			170
F_4				2	36	3	106	22	11		180
F_5			3	32	13	21	13	1	3		86
F_6			14	118		12	7				151
95				P_1		P_2					
WS1809/Thatcher							F_1				
F_2				2			140				159
F_3				2	1	5	50	60	3		121
F_4				4	2	7	115	31	6		165
96		P_1					P_2				
WS1812/Manitou						F_1					
F_2		20	4	17		3	33	28	29		134
F_3		11	4	10	5			1	2		33
F_4	71	45	12	16	4		15		1		164
F_5	22	66	16	27							131
F_6 (5 races)	36	65	16	5							122
97		P_1						P_2			
WS1812/Shortana							F_1				
F_2		19	3	10		4	30	27	22		115
F_3		7	2	1				5			15
F_4	31	26	9	13	3			2	3		87
F_5		24	22	38		3	16	2			105
F_6 (5 races)	10	86	25	29	1						151

Table 11 (continued)

Identification of crosses	Number of plants for each infection type										Total
	Resistant					Intermediate		Susceptible			
	V	00	0-	0	1-	1	2	3-	3	4	
98 WS1812/Thatcher		P_1				P_2	F_1				
F_2	2	10	5	12	1	3	33	54	29		149
F_3		7	2	3			2	1			15
F_4	49	109	17	17							192
F_5		75	44	28	1		3				151
F_6 (5 races)	12	42	20	27							101
99 Leeds/Wells										P_1/P_2 F_1	
F_2								5	38	26	69
F_3									5	20	25
F_4								12	43	12	67
F_5							46	31	22	3	101
F_6							38	13	1		52
100 Wells/Leeds										P_1/P_2 F_1	
F_2								2	41	37	80
F_3									9	20	29
F_4								3	44	19	66

Table 12. Development of resistance to stripe rust as a result of selection and selfing of segregating populations of 43 spring wheat crosses.[1]

Identification	Infection type						Total No. of plants tested
	Resistant		Intermediate		Susceptible		
	Number	Percent	Number	Percent	Number	Percent	
Parents[2]	40	46.5	28	32.6	18	20.9	86
F_1	4	9.3	15	34.9	24	55.8	43
F_2	875	14.7	1,739	29.3	3,324	55.9	5,938
F_3	959	28.7	959	28.7	1,422	42.6	3,340
F_4	2,405	40.5	1,759	29.6	1,770	29.8	5,934
F_5	3,982	70.1	1,048	18.5	650	11.4	5,680
F_6	3,955	88.2	504	11.2	23	0.5	4,482

[1] Crosses number 56 through 98 listed in Table 11.

[2] Total of 86 because of two parents for each cross. Each parent was used several times.

There was a continual increase of resistant types -- from 14.7 percent in the F_2, to 28.7 percent in the F_3, to 40.5 percent in the F_4, to 70.1 percent in the F_5, and to 88.2 percent in the F_6. It should be possible to further shift the distribution towards greater resistance with continued selection and selfing. Intermediate types made up 29 percent of the F_2, F_3, and F_4 populations and eventually decreased to 18.5 percent and 11.2 percent for the F_5 and F_6 generations, respectively. The same percentage of intermediate types in the F_2, F_3, and F_4 was probably due to a shifting of the plant reaction types for the intermediate to resistant class as well as from the susceptible to the intermediate class. There was a continual decrease in the susceptible types from 55.9 percent in the F_2, to 42.6 percent in the F_3, to 29.8 percent in the F_4, to 11.4 percent in the F_5 and to 0.5 percent in the F_6 (Table 12). Thus, the susceptible types were essentially eliminated by the F_6 with only 23 out of 4,482 plants being susceptible.

The 9 spring wheat crosses which did not have resistant progeny in the F_1, F_2 (1,197 plants) and F_3 generations were considered to lack major specific genes for resistance. From a total of 1,578 F_4 plants, 62 (3.9 percent) were resistant, 499 (31.6 percent) were intermediate, and 1,017 (64.4 percent) were susceptible (Table 13). Once the resistant types were obtained in the F_4 (3.9 percent), they increased to 12.7 percent in the F_5 and 59.9 percent in the F_6. There also was a continual decrease in susceptible types from 77.3 percent in the F_2 to 2.5 percent in the F_6. Because of the lack of resistance in the F_2 and F_3, the progress made by selecting and selfing the progeny of these 9 crosses is more dramatic than the rapid increase in resistant types in the other 34 spring crosses. It clearly demonstrates that resistant plants can be selected in crosses from parents which have moderate levels of resistance or are susceptible. Once the resistant plants are found in the F_4 the filial populations are shifted to the resistant type. It should be possible to further shift the distribution towards greater resistance with continued selection and selfing.

The parents -- F_1, F_2, F_3, and F_4 -- progeny of the 2 *T. durum* crosses (99, 100) were susceptible (Table 11). In the F_5 of cross number 99, 46 (45.5 percent) intermediate plants were recovered and 38 (73 percent) were recovered in the F_6 generation. No F_5 or F_6 data is available for cross number 100. This is a good indication

Table 13. Development of resistance to stripe rust as a result of selection and selfing of segregating populations of 9 spring wheat crosses which lacked resistant progeny in the F_2 and F_3 populations.[1]

Identification	Infection type						Total No. of plants tested
	Resistant		Intermediate		Susceptible		
	Number	Percent	Number	Percent	Number	Percent	
Parents	2	11.1	11	61.1	5	27.8	18
F_1	-	-	2	22.2	7	77.7	9
F_2	-	-	271	22.6	926	77.3	1,197
F_3	-	-	186	26.5	517	73.5	703
F_4	62	3.9	499	31.6	1,017	64.4	1,578
F_5	145	12.7	495	43.3	504	44.1	1,144
F_6	521	59.9	327	37.6	22	2.5	870

[1] Crosses number 74, 77, 79, 82, 87, 88, 89, 92 and 94.

that progress can be made even with highly susceptible parents. The progress is not as dramatic, but it is still achieved.

There were 9 crosses -- 57, 58, 60, 61, 62, 67, 69, 84, and 96 -- which had all resistant plants (1,466) in the F_5 generation (Table 11). The F_6 plants of these crosses were inoculated with 5 races. Only 28 (2.17%) of the plants evaluated in the F_6 (1,286) were classified as intermediate. Thus, the resistance selected with 2 races was stable when inoculated with 5 races.

VIII. Field Evaluation of F_2 and F_3 Generations of the Spring Wheat Crosses

Materials and methods. The F_1 hybrid seed of the spring wheat crosses was grown in the field for F_2 seed production. Thirty F_2 populations were planted and rated in 1975 according to the procedures outlined in the general materials and methods. One F_2 population was named "F_2 mix" because it was a general bulk population which contained F_2 seed from all the F_2 populations. Data on the F_3 plants were not collected because the plants were not space planted and were too close together for individual readings. Twenty heads were tagged and harvested for each F_3

population based on head and flagleaf reaction to stripe rust.

Results and discussion. For each of the 30 F_2 populations, a minimum of 72 plants, up to a maximum of 138 plants, with an average of 94 plants were evaluated. Out of 2,819 individual plants, 1,793 (63.6 percent) were susceptible, 1,009 (35.8 percent) were intermediate in reaction, and 17 (0.6 percent) were classified as resistant (Table 14). Comparisons between the F_2 and F_3 are not possible because of the lack of individual plant readings in the F_3. A higher level of resistance was expressed in the F_2 populations of the spring wheat in comparison with the winter wheats. The plants with intermediate reaction types made up 35.8 percent of the total population with the spring wheats and only 19.9 percent with the winter wheats. This was expected because of the higher levels of resistance found in the spring wheat parents compared to the winter wheat parents (Table 8). Since the percentage of intermediate types moved up to 51.2 percent for the F_3 populations of the winter wheats, it was assumed that the spring F_3 populations would have moved even further.

Table 14. Results of field observations of F_2 populations of spring wheat crosses.

Identification of crosses	Number of plants for each disease rating		
	Resistant	Intermediate	Susceptible
56-2 Bonanza/Centana	0	35	55
47-2 Bonanza/Manitou	0	43	44
59-2 Bonanza/Sheridan	0	51	25
60-2 Bonanza/Thatcher	1	38	41
61-2 Bonanza/WS 1809	0	71	9
62-2 Bonanza/WS 1812	14	71	17
63-2 Centana/Bonanza	1	34	44
64-2 Centana/Polk	0	7	65
65-2 Centana/WS 1809	0	44	43
66-2 Centana/WS 1812	0	9	74
67-2 Fortuna/Bonanza	0	50	47
68-2 Fortuna/Centana	0	1	112
69-2 Fortuna/Manitou	0	30	50
72-2 Fortuna/Shortana	0	14	92
73-2 Fortuna/WS 1812	0	24	80
74-2 Manitou/Centana	0	17	69
75-2 Manitou/Polk	0	50	43
76-2 Manitou/Shortana	0	24	57
77-2 Manitou/Thatcher	0	57	52

Table 14 (continued)

Identification of crosses	Number of plants for each disease rating		
	Resistant	Intermediate	Susceptible
78-2 Polk/Shortana	0	31	75
79-2 Sheridan/Centana	0	5	92
80-2 Sheridan/Manitou	1	62	35
82-2 Sheridan/Shortana	0	0	102
84-2 Sheridan/WS 1812	0	25	83
85-2 Shortana/Bonanza	0	49	32
86-2 Shortana/Centana	0	1	92
87-2 Shortana/Thatcher	0	27	71
88-2 Shortana/WS 1809	0	61	41
91-2 Thatcher/Polk	0	38	53
F_2 Mix	0	40	98
Total	17	1,009	1,793
Percent of total population	0.6	35.8	63.6

The best 10 crosses based on percentage of individuals in the intermediate class were: Number 62, Bonanza/WS 1812 (84 percent); number 61, Bonanza/WS 1809 (89 percent); number 59, Bonanza/Sheridan (67 percent); number 80, Sheridan/Manitou (63 percent); number 85, Shortana/Bonanza (60 percent); number 88, Shortana/WS 1809 (60 percent); number 75, Manitou/Polk (54 percent); number 67, Fortuna/Bonanza (52 percent); number 77, Manitou/Thatcher (52 percent); and number 65, Centana/WS 1809 (51 percent). As with the winters, the "general combining ability" was calculated and the 10 common wheat varieties are listed in order according to "general combining ability" in Table 10 . WS 1809, Bonanza and Manitou are ranked first followed by an intermediate group of Thatcher, Polk, WS 1812, Sheridan, and Shortana. Fortuna and Centana are on the bottom of the scale (Table 10). This is consistent with the ranking of the 10 best crosses. The 3 crosses with WS 1809 in the parentage are in the best 10. Five of the 9 crosses with Bonanza in the parentage are in the best 10. Three of the 7 crosses with Manitou in the parentage are in the best 10.

GENERAL DISCUSSION

Several studies were undertaken to determine the gene action involved in the minor gene lines (P.I. 178383/Itana//commercial variety) and to determine if this resistance can be manipulated in a conventional breeding program. The studies involved in intercrossing these minor gene lines were described above. In the first study a high level of resistance was selected in the F_2 and maintained in the F_3 segregating progeny when intercrossing minor gene lines (P_1/P_2). This high level of resistance was also maintained in the second study when intercrossing F_1 minor gene lines ($P_1/P_2//P_3/P_4$). The 2 diallels of the minor gene lines demonstrate a high percentage of additive gene action and high heritabilities involved in the resistance of these advanced lines. The presence of this additive gene action and high heritabilities clearly indicates that this resistance can be easily manipulated and selected for in a breeding program.

After intercrossing the minor gene lines with commercial varieties, it was postulated that the commercial varieties carried minor genes (96, 99). Thus, the next logical step in the development of this resistance would be to cross cultivars which are commercially acceptable. By utilizing acceptable commercial varieties as parents, undesirable agronomic traits associated with sources of newly introduced germplasm would be avoided. The description and results of the intercrossing of 10 winter wheats and 10 spring wheats and the selection for resistance on their progeny were presented. The data from the greenhouse and field work demonstrated that selection for transgressive segregation for stripe rust resistance was achieved. Transgressive segregation for intermediate or moderate resistance was found in the F_4 progeny of all 38 winter wheat crosses evaluated in the greenhouse. In the field progress towards increased resistance was demonstrated with 35 winter wheat crosses which were evaluated for 2 years. Transgressive segregation for resistant plants in the F_2, F_3, F_4, F_5, and F_6 generations was demonstrated for the 43 spring wheat crosses. Resistance was stable in 9 spring wheat crosses when the F_6 progeny were inoculated with 5 races. In 9 spring wheat crosses which did not have resistant plants in the F_2 and F_3, transgressive segregation was found in the F_4, F_5, and F_6 generations.

These 9 spring wheat crosses and the 31 winter wheat crosses which lacked resistant progeny in the F_2 and F_3 generations are important crosses for support of described methods of resistance development. In previous work, minor gene resistance from P.I. 178383 was obtained in the F_3 generation. From a total of 1,431 F_3 plants, 27 (1.9 percent) were resistant, 156 (10.9 percent) were intermediate, and 1,248 (87.2 percent) were susceptible (51). After further selection and development, resistance in these minor gene lines (P.I. 178383/Itana) was combined with commercial wheat varieties to develop another group of minor gene lines (P.I. 178383/Itana//commercial wheat variety)(99). In contrast to previous work, the present resistance was developed from completely susceptible parental material and thus was accumulated more slowly.

In conclusion, the selection for resistance from crosses of susceptible commercial varieties has been demonstrated to be a valid method for the selecting and building up of new sources of resistance which have been overlooked or selected against in the past. Once the resistance is built up it can be manipulated as demonstrated with the additive, minor-gene lines. This resistance is probably of the general type because of the results of inoculations with 5 races of stripe rust even though it cannot be definitely demonstrated at the present time. Because of the good agronomic types that were involved in the parentage of these progeny, good agronomic types can probably be selected from space-planted advanced bulk populations of the resistance material.

The demonstration of obtaining resistance from susceptible cultivars emphasizes potential future uses. Many potential sources of resistance may have been inadvertently discarded in the past because they were not detected in the F_2 and F_3 generations. Careful observation and selection through the F_4 generation will facilitate the detection of new sources of resistance. More studies with this type of resistance should be undertaken in the future. The type of gene action and the number of genes involved should be studied in more detail. New ways of accumulating and manipulating this type of resistance should be explored. The future looks rather promising.

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