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THE ADDITION OF STEM RUST RESISTANCE TO GLENLEA FROM *Triticum timopheevi* ZHUK. AND WHEAT-RYE-TRANSLOCATION STOCK

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Richard V. Ndondi

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TABLE OF CONTENTS

CHAPTER PAGE

LIST OF TABLES

TABLE PAGE

LIST OF FIGURES

ABSTRACT

The objective of the present investigation was to determine the nature and mode of inheritance of resistance factors present in the resistant varieties (WRT) ND71-13-1066, Line W (W3563) and Glenlea, and to transfer resistance genes from Line W (W3653) and (WRT) ND71-13-1066 into Glenlea.

The three resistant lines were analyzed genetically on the basis of ratios obtained in F2, F3 and BC1F2 populations of crosses and backcrosses to the susceptible variety W3498 when tested with wheat stem rust races C25(38), C65(38), C49(15) and C33(15B-1L).

The results indicated that Glenlea possesses one recessive gene, (WRT) ND71-13-1066 has two dominant genes and Line W (W3563) has one dominant gene conferring resistance to the four stem rust races.

The SrTt2 gene from Line W (W3563) was transferred into Glenlea and the resistant line derived from the cross between these two varieties was designated Glenlea-T.

The Sr27 gene from (WRT) ND71-13-1066 was also transferred into Glenlea by crossing and backcrossing to Glenlea. The resistant line carrying Sr27 gene from the cross between these two varieties was designated Glenlea-R.

INTRODUCTION

Much of the stem rust resistance in commercial common wheat, *Triticum aestivum* L. cultivars has been derived from other species. McFadden (1949) reported that the varieties of common wheat first grown in the United States lacked sufficient rust resistance to prevent losses in years of heavy epidemics and that prior to 1916, resistance to stem rust *Puccinia graminis* Pers. f. sp. *tritici* Eriks. and E. Henn. did not exist in any of the varieties grown in the United States. Hayes (1920), Bailey (1928), Güssow (1933) and Greaney (1933) have reported on the occurrence of stem rust epidemics in the United States and Western Canada between the years 1916 and 1933 which caused enormous grain and financial losses. Peturson (1958) reported that stem rust resistant wheats were first introduced into Western Canada in 1936. Since then, much effort has been aimed at identifying resistance sources in common wheat cultivars and from alien germ plasm. Alien germ plasm is defined as germ plasm from a species related to a crop species; in a narrow sense germ plasm is considered as alien only if the two species involved are sufficiently distinct that they show some degree of genetic isolation (Knott and Dvorak 1976). McFadden (1949) pointed out that it has been widely recognized for a long time that certain varieties of einkorn, emmer, durum and poulard wheat showed marked resistance to one or more of the rusts and that Carleton (1901) appears to

have been the first to suggest the possibility of transferring rust resistance from the tetraploid durum and emmer wheats to common wheat through cross breeding. Dvorak (1977) reported that the wild cultivated relatives of common wheat have been used successfully as sources of resistance to a number of wheat pathogens.

Watson (1970) and Kerber and Dyck (1969) reported that there are valuable genes in the immediate diploid relatives of common wheat; these include *T. monococcum* L. (2n = 14 = AA), *Aegilops speltoides* Tausch. (2n = 14 = BB) and *Aegilops squarrosa* L. (2n = 14 = DD). Knott and Dvorak (1976) noted that the tetraploid *Triticum* species carried more resistance to rusts and other diseases than did the hexaploid bread wheat. Thus, some of the early work with interspecific crosses involve hybrids of the tetraploid emmers, *T. dicoccum* and durums, *T. durum*. Other sources of alien stem rust resistance have been from the genera *Aegilops*, *Agropyron* and *Secale*, [Gerechter Amitai *et al.* (1971); Knott (1961, 1971); Acosta (1962)]. Watson (1970) and Knott (1971) pointed out that these species have a particularly high degree of resistance and the resistance covers a wide range of wheat stem rust races.

It was, therefore, desirable to utilize the valuable alien stem rust resistance from rye, *S. cereale* and *Triticum timopheevi* Zhuk. in a breeding program aimed at increasing the number of effective resistance genes in the common wheat, *T. aestivum* cv Glenlea. Glenlea is resistant to all known stem rust races now present in Canada (Evans *et al.* 1972). Modern breeding concepts are such that varieties are bred to contain one or more genes for specific

resistance and that additional genes for resistance are transferred from donor parents to a recipient commercial variety, that is already protected by one or more genes. Watson (1970) reported that in common wheat, single genes for resistance do not provide long lasting stability and that it is now apparent that combinations of genes are superior in this regard. The more genes for resistance in a particular host, the less likely it is to be made susceptible by a mutation in the pathogen.

2. LITERATURE REVIEW

2.1 Sources of Alien Stem Rust Resistance

2.1.1 *Triticum durum* Desf.

McFadden (1949) reported that certain varieties of durum showed marked resistance to a number of rusts and that early efforts were made to incorporate stem rust resistance from durum wheat into common wheat. Hayes (1920) crossed the common wheat cultivar Marquis with the stem rust resistant Iumillo durum originally from Southern Russia and obtained the resistant derivative Marquillo which became a commercial variety in the Red River Valley of Minessota and North Dakota. From the double cross (Kanred X Marquis) X (Iumillo X Marquis), Hayes obtained the famous stem rust resistant variety, Thatcher, and its sister line, Double Cross (Hayes *et al.* 1936; Harrington *et al.* 1938). Watson and Stewart (1956) reported that the Australian cultivars Gabo and Timstein, together with the American variety Lee, were developed from a cross involving the stem rust resistant Gaza durum. (Bobin^2 X Gaza = Gabo, Bobin^2 X Gaza = Timstein, Hope X Timstein = Lee = Hope X (Bobin^2 X Gaza). The resistance gene from Gaza durum present in Gabo, Timstein and Lee is designated Sr11.

2.1.2 *Triticum dicoccum* Schrank.

In 1920, McFadden (1949) in South Dakota succeeded in isolating common wheat lines highly resistant to both stem and leaf rust and several other diseases from a cross between Marquis and Yaroslav emmer *T. dicoccum* Schrank. Two of the segregates, Hope and H44, were practically immune to stem rust in the mature plant stage. Both Hope and H44 have been widely used as parental material in crosses that have given rise to rust resistant varieties that are now grown extensively in the spring wheat region of United States and Canada. Harrington (1938) produced the stem rust resistant variety Apex from the triple cross (H-44-24 X Double Cross) X Marquis while Rescue was produced by Platt from the cross S.615 X Apex (Harrington *et al.* 1938).

Jakubziner (1962) reported that forms excelling in stem rust resistance were found among the Indian Khapli variety and Volga groups: Yaroslav emmer and Vernal varieties. These varieties played an outstanding role in breeding for immunity to wheat stem rust. He pointed out that in Czechoslovakia the Khapli variety is resistant to most stem rust races except race 50 and that in the Soviet Union the excellent hard wheat variety Harkovskaia 46 and the varieties Raketa and Caesium 94 approved for Eastern and Western Siberia respectively were produced using *T. dicoccum* as a crossing partner. He concluded that in recent years new areas in the virgin lands have been conquered due to resistance from *T. dicoccum*.

2.1.3 *Triticum boeoticum* Boiss.

Gerechter-Amitai *et al.* (1971) reported that in

screening tests for stem rust resistance, promising plants were found in each of the two diploid progenitors of common wheat: *T. boeoticum* Boiss. and *A. speltoides* Tausch. They transferred stem rust resistance from *T. boeoticum* Boiss. to the susceptible Mindum and Spelmar varieties of cultivated *T. durum* using race 14 as a test race. They reported that the F3 and F4 progenies included segregants which displayed seedling resistance to races 17, 19, 21, 40, 53, 194, 222, 315 and 322, and that stem rust resistance to race 14 was controlled by a single dominant gene. The gene from einkorn is designated as Sr 21.

2.1.4 *Triticum monococcum* L.

Kerber and Dyck (1973) transferred stem rust resistance from *T. monococcum* L. to tetraploid and hexaploid wheat by means of interspecific hybridization and genetic recombination. They first transferred stem rust resistance from *T. monococcum* cv RL 5244 to *T. durum* cv Stewart by five backcrosses to the susceptible variety Stewart using race 15B-4 as the test race. The resistant form resulting from the backcrosses was designated as Stewart-R. They then transferred the *monococcum* resistance to a susceptible common wheat, *T. aestivum* cv Marquis, by crossing Stewart-R with Marquis and using race 15B-4 as the test race. The resistant hexaploid form derived from three backcrosses to Marquis was designated Marquis-R. They also studied the inheritance of the *monococcum* resistance at the diploid, tetraploid and hexaploid levels in crosses with a relatively susceptible diploid cultivar

RL 5317, Stewart and Marquis, respectively. They reported that a single gene designated Sr 22 conferred resistance.

2.1.5 *Agropyron*

Knott (1961, 1971) and Wienhues (1963) reported that among all genera related to common wheat, *Agropyron* has a special resistance against all known biotypes of stem rust. Shebeski (1939) made successful crosses between the common wheat variety Chinese Spring and *A. elongatum* (Host) Beauv. in an attempt to transfer stem rust resistance into common wheat. A number of lines developed from the intergeneric cross Chinese Spring X (Chinese Spring X *A. elongatum*) include PW327, PW357 and S44-2-7 which showed a high degree of stem rust resistance to a mixture of races under artificial epidemic conditions at the University of Saskatchewan. Shebeski and Wu (1952) studied the inheritance in common wheat of stem rust resistance derived from *A. elongatum* (Host) Beauv. using line PW357-5 as a source of resistance in crosses with Apex, Thatcher and Red Egyptian. They reported that the resistance was dominant and governed by three complementary genes. Knott (1961) transferred stem rust resistance from *A. elongatum* (Host) Beauv. to the common wheat variety Thatcher using the wheat-*Agropyron* derivative PW327 (Perennial Wheat 327) produced by Shebeski. He crossed PW327 to the variety Thatcher and tested the backcross derivatives with races 56 and 15B. He found that the *Agropyron* resistance to stem rust proved to be dominant. He also made irradiation experiments and obtained seven translocation lines which were resistant to races 56 and 15B. One of the translocations, line 3-3-1, had an *Agropyron*

gene that interacted with Sr7 giving a 0;-1 infection type while when alone the two genes conditioned 2- and 1+ infection type, respectively. The combination of the two had an additive effect.

Elliot (1957) crossed the resistant octoploid (*A. elongatum* X hexaploid wheat) derivative SH 198-4 with the susceptible hexaploid spring wheat variety Idaed and obtained F1 seed which he irradiated and finally obtained a rust resistant line, Selection 11244. Knott *et al.* (1977) transferred stem rust resistance from a wheat-*A. elongatum* derivative, line A28 into the common wheat variety Marquis. Resistance was found to be carried on *Agropyron* chromosome $7el_2$ which also carries a gene that results in a high level of yellow pigment in the flour. Wienhues (1963) transferred stem rust resistance of *A. intermedium* to common wheat. The stem rust resistance genes Sr24, Sr25 and Sr26 have all been obtained from the genus *Agropyron* and are now in a number of common wheat cultivars (Knott and Dvorak 1976).

2.1.6 *Triticum timopheevi* Zhuk.

The tetraploid wheat, *T. timopheevi* Zhuk. (2n = 28) has been considered a valuable source of resistance to a number of bread wheat pathogens (Shands 1941; Hart 1943; Jakubziner 1962; McIntosh and Gyarfas 1971). Knott and Dvorak (1976) reported that *T. timopheevi* Zhuk. probably has more disease resistance than any of the other *Triticum* species; consequently there has been considerable interest in using it as a source of resistance. Pridham (1939) crossed the common wheat variety, Steinwedel, with *T. timopheevi*

and obtained common wheatlike lines that were resistant to stem rust and leaf rust. Shands (1941) reported that the first cross from which fertile hybrids were secured was made in 1933 between the spring wheat selection 2666A2-2-15-6-3 from a hybrid of Illinois No. 1 X Chinese and *T. timopheevi* PI 94761. Allard (1949) transferred *timopheevi* disease resistance from the strain PI 94761 brought to the United States by Dickson to an unnamed spring wheat selection out of the hybrid Illinois No. 1 X Chinese CI 6223 designated 2666A2-2-15-6-3 by the Wisconsin Agricultural Experiment Station. Two of the selections are CI 12632 and CI 12633. He reported that the inheritance of the *timopheevi* resistance was relatively simple, perhaps depending on not more than two major genes. Allard and Shands (1954) reported that the stem rust resistance of the two hard red spring wheat-*T. timopheevi* selections, CI 12632 and CI 12633, in hybrids with Reward and Marquis is governed by dominant duplicate genes which are linked with a recombination value of 14.78 $\pm$ 1.75 percent. Nyquist (1957) located the resistance genes of CI 12633 on chromosome XIII (2B). Nyquist (1962) crossed CI 12633 which he described as being immune to all races present to five susceptible cultivars: Ramona CI 8241-1, Federation CI 4734, White Federation CI 4981, Chinese Spring CI 6223 and 2666A2-2-15-6-3 and concluded that stem rust resistance was controlled by one gene and that differential fertilization was at least partly responsible for the different ratios obtained.

Watson and Stewart (1956) compared the rust reaction of *T. timopheevi* derivatives CI 12633 and W1309 with wheat varieties

Gabo, Timstein, Lee and Gaza durum to stem rust races 126 Anz, 222 Anz and leaf rust races 26 and 135. They reported that Gabo, Timstein and Lee behaved similarly to both stem and leaf rust but had no similarity to the *T. timopheevi* derivatives. The results indicated that Timstein, Gabo and Lee derived their resistance from Gaza durum. Watson and Luig (1958) reported that genuine Steinwedel X *T. timopheevi* material has been available in Australia since 1939 from the cross originally made by Pridham. One of the selections was named Timvera (Sydney University Accession W1308). Timvera, together with its two sibs W1309 and W1310, showed high resistance to many of the local strains of stem rust.

Semeniuk (1947) studied chromosomal stability in certain stem rust resistant derivatives from the cross made by Pridham between Steinwedel, a soft white common wheat and *T. timopheevi*. He reported that it was possible to select lines which combined high chromosome stability, common wheat characteristics and resistance to stem and leaf rust. Atkins (1967) studied the inheritance of reaction to race 15B of wheat stem rust in derivatives of Frontana and Shands 473 (*T. timopheevi* X Cheyene CI 13005) in crosses with three susceptible varieties Comanche, Iowin and CI 13279 (Iowa 5373). He reported that the high level of stem rust resistance in Shands 473 was governed by a single recessive gene. Newton *et al.* (1940) reported on the seedling reaction of *T. timopheevi* Zhuk. to 20 physiologic races of *P. graminis tritici* including race 15B. The species was highly resistant to all 20 races. McIntosh and Gyarfas (1971) assessed the range of variability

in stem rust reaction among accessions of *T. timopheevi* and that available in a group of common wheat stocks having genes derived from *T. timopheevi*, CI 12632 (W1656), Timvera (W1308), CI 13005 and Line W (W3563) using *P. graminis* cultures of North America and Australian origins. They reported that CI 13005 appears to have at least two genes for low reaction, one in common with CI 12632 (W1656) and Timvera (W1308). Line W (W3563) produced a low infection type (0;) which was easily distinguished from that characteristic of CI 12632 indicating that the gene present in CI 12632 is not present in Line W (W3563). McIntosh and Gyarfas (1971) concluded that variability in *T. timopheevi* Zhuk. with respect to reaction to stem rust *P. graminis tritici* appears to be restricted to relatively few genes. Three distinct genes derived from the tetraploid appear to be available in common wheat - *timopheevi* derivatives: SrTt1 is present in CI 12632 (W1656) and CI 13005. SrTt2 is present in Line W (W3563) and a third undesignated gene appears to be present in CI 13005.

2.1.7 *Secale cereale*

Rust resistance has been reported to be present in rye, *S. cereale*, (Kerber and Dyck 1969; Knott 1971; Knott and Dvorak 1976; Luig and Watson 1976). McIntosh (1973, 1976) reported that stem rust resistance derived from rye is available in a number of common wheat cultivars. A rye translocation to chromosome 1B or substitution of 1R for 1B has been widely used in Europe and Russia in the cultivars Zorba, Weigue, Mildress, Aurora and others. Wheat-

rye-translocation lines involving rye chromosomes carrying stem rust resistance in wheat background are now in use; these include WRT-1 which carries gene Sr27 from Imperial rye 3A/R, WRT-2 carries stem rust resistance from Imperial Rye X Shephard 1D/R, WRT 1B/1R widely used in Europe and Russia, and Acosta wheat (WRT238-5) Chinese Spring X Imperial Rye. Acosta (1962) reported transferring stem rust resistance from rye to wheat by X-raying crosses between the wheat variety Chinese Spring and the rye variety Imperial. It was designated WRT238-5. WRT238-5 is highly resistant to the prevalent races of stem rust in the United States, as well as to some uncommon races which are virulent on germ plasm stocks widely used as sources of stem rust resistance. WRT238-5 resistance is in the background of the common wheat varieties Pembina, Justin, Selkirk and Thatcher. Stewart *et al.* (1968) reported that seedlings of two homozygous translocation lines 238-5-17 and 238-5-29 involving a portion of a rye chromosome, *S. cereale* cv Imperial, in the genetic background of the wheat variety Chinese Spring were highly resistant to eight cultures of *P. graminis tritici* race 15B at 18, 24 and 29 C temperature. They also tested three wheat-rye backcross derived lines of Justin, Pembina and Selkirk for reaction to three cultures of rye stem rust, cultures A059, A-67 and B-39, all virulent on rye, and three isolates of wheat stem rust (two isolates of race 32B and race 151) using Marquis wheat and Prolific rye as check varieties. They reported that all backcross derived lines were either resistant or had no visible signs of infection to the three cultures of rye stem rust, whereas Prolific was susceptible. They also reported

that seedling plants of line 238-5-29 X Pembina^5 were tested at Njoro, Kenya in 1965 using bulk inoculum of races 11, 21, 34, 40ES, 40T, 295 and 296. Fourteen plants out of a total of 22 were highly resistant, with 0; infection type. Seedling tests with progenies from the cross WRT238-5-29 X Pembina^5 showed resistance to all current races in Kenya. Luig and Watson (1976) reported that Acosta's translocation line WRT238.5 and its derivative line 177 (W2691/ WRT238.5), as well as the addition line G70, showed low infection types when inoculated with about 1000 Australian collections representing about 35 different strains of wheat stem rust. The factor for resistance in the rye segment has been designated Sr27 (McIntosh 1973). Luig and Watson (1976) reported that their results further suggested that a broad resistance to *P. graminis* in wheat-rye translocation lines existed.

2.2 Methods of Transferring Alien Stem Rust Resistance to Common Wheat

Related species and genera of common wheat provide a source of genes for disease resistance and other characters of economic importance (Morris and Sears 1967). The incorporation of genes for disease resistance into common wheat requires the transfer of chromatin from the donor species. This may involve whole or part chromosomes. There are several methods by which such gene transfers have been effected.

2.2.1 Interspecific Hybridization

The transfer and combination of sets of chromosomes by interspecific crosses; this may involve the use of bridge hybrids (Gerechter-Amitai *et al.* 1971; Shebeski *et al.* 1952; Kerber and Dyck 1973).

2.2.2 Addition Lines

Involves the addition of a chromosome to the normal chromosome complement of common wheat. Addition lines have a complete complement of wheat chromosomes plus one or more alien chromosomes; they may be monosomic or disomic for the added chromosome (Riley *et al.* 1958; Knott 1964; Morris and Sears 1967).

2.2.3 Substitution Lines

Involves the subtraction of a chromosome from the normal chromosome complement of wheat and replacing it with an alien chromosome. It essentially involves substituting a pair of alien chromosomes for a pair of wheat chromosomes (Morris and Sears 1967). Larson and Atkinson (1970, 1973) reported on a wheat-*Agropyron* triple alien chromosome substitution line, T-Ae, in which *Agropyron* chromosomes have replaced wheat chromosomes 4D, 5D and 6D.

2.2.4 Translocation Breeding

A segment of an alien chromosome can be transferred to a wheat chromosome through induced breakage and interchange of chromatin segments or through crossing over. Ideally, the alien chromosome segment should be as small as possible particularly if the two species show extensive genetic and chromosomal differentiation

(Knott and Dvorak 1976). Translocation breeding is accomplished by means of irradiation or the use of appropriate pairing and synapsis promoters to induce translocations and increase the frequency of breakage and interchange of chromatin segments (Morris and Sears 1967). Induced translocations between a wheat chromosome and the alien chromosome may involve exchanges of terminal segments or by an intercalary translocation. Irradiation methods used include X-rays, gamma rays, thermal neutrons, Cobalt-60 and the irradiated material include plants, spikes or seeds. Sears (1956), Elliott (1957), Knott (1961), Sharma and Knott (1966) and Acosta (1962) have all produced translocation stocks carrying stem or leaf rust resistance.

2.2.5 Chromosome 5B Method

Many attempts to exploit the disease resistance of species that are closely related to common wheat have failed due largely to the inherent diploidizing system in wheat that prevents pairing between homoeologous chromosomes but allows homologues to pair normally. Under such a system, at meiosis in interspecific hybrids there is no pairing, synapsis or recombination between the wheat and alien chromosomes and therefore, the incorporation of alien segments small enough to include only the desired allele becomes almost impossible (Riley 1966; Riley *et al.* 1968).

Riley (1966), Riley and Kimber (1966), Morris and Sears (1967), Riley, Chapman and Johnson (1968), Knott (1971) and Sears (1976) have reported that transfers of desirable genes from

other species or genera to wheat are made possible by the use of 5B deficient (Nullisomic 5B) wheat plants in the crosses. Wall, Riley and Chapman (1971) and Sears (1975, 1976) have reported that induced homoeologous-pairing (ph) mutants may now be used instead of wheat plants nullisomic for 5B. Alien genomes such as *A. speltoides*, *A. mutica* and *A. longissima* also promote pairing. Riley (1966) and Sears (1976) reported that in hybrids with *T. aestivum* these promoters raise the pairing potential of homoeologues.

2.2.6 Mutations

Spontaneous and induced mutations at localized points in chromosomes may result from irradiation or the use of chemicals such as mustard gas, ethylene oxide, diethyl sulfate, or EMS. Mutagenic agents are considered a feasible approach in attempting to obtain rust-resistant mutants (Morris and Sears 1967; Konzak 1956, 1973; Hasim 1974).

2.3 Problems Involved in the Utilization of Alien Stem Rust Resistance

Efforts to utilize alien stem rust resistance have often met with disappointments. Some of the problems encountered in transferring resistance from alien sources to common wheat are typical of interspecific corsses; these include sterility, incompatability, linkage, transmission and dilution.

2.3.1 Sterility

Hayes (1920) reported that the F1 plants obtained

from the crosses between Marquis with *T. durum* cv Mindum and Kubanka CI 2094 and emmer (Emmer Minn. 1165) had a large percentage of shrivelled and abortive pollen grains. McFadden (1949) found that the two main problems in the cross Marquis X Yaroslav emmer were sterility in F1 and linkage between undesirable emmer characteristics and disease resistance. Allard and Shands (1954) pointed out that crosses involving *T. timopheevi* and common wheat are highly sterile. Kerber and Dyck (1973) reported that the cross between *T. monococcum* cv 5244 and *T. durum* cv Arnautka was incompatible despite repeated attempts. The and Baker (1975) reported on the crossability of durum and hexaploid wheats with einkorn. They found that durum wheat cultivars, Glossy Huguenot and Marruecos, differed in crossability with einkorn. The hexaploid wheat cultivars, Steinwedel, Hope and Timstein, had very poor crossability with einkorn in comparison with Chinese Spring. They attributed the differences to genetic, technical and environmental factors. Triploid F1 hybrids (AAB) displayed normal germination and survival while tetraploid AABD hybrid grains had low germination and survival rates. The hybrids were male sterile, and although anthers were formed, they were never observed to dehisce.

2.3.2 Maturity

Allard and Shands (1954) reported that Shands (1941) transferred the stem rust resistance of *T. timopheevi* to hard red winter wheat selections, but that their value was limited by an association between resistance and late maturity. Allard (1949)

reported that the stem rust resistant *T. timopheevi* derivatives CI 12632 and CI 12633 headed about one day later than Thatcher at Madison, Wisconsin. Nyquist (1962) compared the mean heading date of homozygous stem rust resistant derivatives from CI 12633 X Ramona cross with homozygous susceptible families and found that the homozygous susceptible genotypes were about 12 days earlier in heading time than the homozygous resistant genotypes.

2.3.3 Transmission

Knott (1961) studied the transmission of the translocated *Agropyron* resistance from PW327 through the gametes. He reported that in two cases transmission through the egg was normal but pollen transmission was much reduced (6.7% and 2.2%). In another translocation transmission was not with normal frequency through either the egg (38.1%) or the pollen (20.4%). Nyquist (1962) reported differential fertilization in crosses involving the *timopheevi* derivative CI 12633 with five common wheat varieties.

2.3.4 Linkage

Bailey (1928) reported that in many crosses involving durum, rust resistance was linked with durum characteristics unsatisfactory in a bread wheat. Elliott (1957) reported that the wheat-*Agropyron* rust resistant selection 11244 had red glumes, a dominant condition not present in either parent. Sears (1963) reported that the resistance gene Sr11 from Gaza durum in Timstein was linked with a pollen killer, locus ki. Knott *et al.* (1977) reported that the *Agropyron* chromosome, $7el_2$ carrying stem rust

resistance in the wheat-*Agropyron* derivative A28 like $7el_1$ in Agrus carries a gene that results in a high level of yellow pigment in the flour. Dvorak and Knott (1977) reported that some of the ionizing radiation-induced translocations between alien and wheat chromosomes show no deleterious effects and are transmitted normally through the pollen.

2.3.5 Low Yield

Addition, substitution and translocation lines carrying alien stem rust resistance have been found in some cases to yield less when compared to standard varieties (Wienhues 1963). WRT238.5 in Pembina background when crossed to Neepawa decreased yield by 23 percent (Dyck personal communication; Knott 1971).

2.3.6 Dilution Effect

Kerber and Dyck (1973) studied the inheritance of the *monococcum* stem rust resistance at the diploid, tetraploid and hexaploid levels and found that the effectiveness of this gene (Sr22) was reduced with increasing levels of ploidy. The degree of resistance was progressively diluted from ;1 to 1+ to 2 with each increase in ploidy. Watson and Luig (1958b) reported that Timvera (Steinwedel X *T. timopheevi*), like CI 12632 and CI 12633 (2666A2-2-15-6-3 X *T. timopheevi*), have not inherited all the genes for resistance from the *T. timopheevi* parent.

2.3.7 Susceptibility to New Virulent Races

Watson and Stewart (1956) reported that with the

advent of race 15B several sources of resistance including Gaza durum and *T. timopheevi* became ineffective simultaneously in U.S.A. In Australia the occurrence of races 126 and 222 resulted in the susceptibility of Gaza but *T. timopheevi* remained resistant. Peturson (1958) reported that a significant increase in race 15B of stem rust, which could attack the stem rust resistant varieties Thatcher, Regent, Renown and Apex, occurred in 1952; and during the next three years it occurred in epidemic proportions causing very severe crop losses in Western Canada. Luig and Watson (1976) reported that backcross lines from the cross between WRT238.5 with susceptible cultivars W2691 and W3498 carrying gene Sr27 exhibited high infection types to a synthetic hybrid between *P. graminis tritici* and *P. graminis secalis* and to several strains of *A. scabrum* rust that are putative hybrids between the two formae speciales. Hart (1943) reported that race 189, an unusually virulent race in Peru, can attack seedlings and adult plants of *T. timopheevi*, and race 19 in the United States was moderately virulent on seedlings and on older plants. In 1942, there was 35 percent of stem rust on *T. timopheevi* in certain experimental plots at University Farm, St. Paul, Minnesota. Race 15B was virulent on this species of *Triticum*. These results contrasted with those obtained by Newton *et al.* (1940) who reported that seedling reaction of *T. timopheevi* to race 15B was highly resistant. Hart (1943) stated that it seemed that the Canadian race 15B was different from the race 15B used in the U.S.A. McIntosh and Gyarfas (1971) reported that when the cultivar Mengavi, possessing gene SrTt1, was first released in

Australia in 1958, it was resistant to all known strains. However, at present the majority of predominant strains are virulent on stocks with SrTt1. Wheat lines with gene SrTt2 are resistant to all Australian *P. graminis* cultures at the present time, but are susceptible to certain North American cultures, 15B-51A. They reported that certain 15B cultures of more recent origin are virulent on CI 12632 but not on *T. timopheevi*. United States culture 15B-51A was virulent on stocks with both SrTt1 and SrTt2 (infection type 3+); it also has virulence for additional genes in *T. timopheevi*, as indicated in their investigation.

2.3.8 Obstacles to the Incorporation of Alien Stem Rust Resistance

Attempts to exploit alien disease resistance of many species that are closely related to common wheat have frequently been unsuccessful. This is due to the common wheat diploidizing system that prevents pairing between homoeologous chromosomes but permits homologoues to pair normally. Under such a system, at meiosis in interspecific hybrids, there is no pairing, synapsis or recombination between the wheat and alien chromosomes; and therefore, the incorporation into wheat of alien segments small enough to include only the desired allele becomes impossible. (Riley *et al.* 1968; Sears 1976; Knott and Dvorak 1976). Riley *et al.* (1968) reported that normally in *T. aestivum*, meiotic synapsis is confined to fully homologous partners. Synapsis between homoeologues is prevented by the activity of pairing suppressors. These include the Ph locus on the long arm of chromosome 5B. There are two other suppressors located on the short arm of chromosome 3A and 3D, respectively.

Minor suppressors are on chromosome 3AL, 3DL and 4D. There has been little or no evidence that an alien genome has any effect on chromosome pairing and synapsis (Sears 1976; Riley 1966).

There are also pairing promoting chromosomes that carry genes that promote pairing. These include chromosomes 5BS, 5DL, 5AL, 3BL, 3DL and 2AS (Sears 1976). Alien genotypes that promote pairing have been found in *Aegilops mutica*, *A. longissima* and *A. speltoides*, which carry an allele that is dominant to the Ph (pairing homoeologous) locus on chromosome 5BL that normally prevents synapsis (Riley 1966; Sears 1976). Thus, in attempting to induce homoeologous recombination between an alien chromosome and a wheat chromosome, material can be used that is deficient for chromosome 5B, mutant ph, or a system that incorporates *A. speltoides* which suppresses the activity of 5BL (Wall *et al.* 1971; Riley *et al.* 1973; Sears 1976).

2.4 Procedures used to Determine the Number and Nature of Alien Stem Rust Resistance Genes

The presence of resistance genes in alien cultivars is determined by testing with a number of stem rust races. Gerechter-Amitai *et al.* (1971) reported that in screening tests for stem rust resistance, promising plants were found in *T. boeoticum* and *A. speltoides*. McIntosh and Gyarfas (1971) reported assessing the range of variability in stem rust reaction among 22 *T. timopheevi* accessions using *P. graminis* cultures of North America and Australian origins. Cultivars carrying resistance genes are normally crossed

and backcrossed to susceptible cultivars and the number of resistance genes are determined by genetic analysis of segregating populations (Shebeski and Wu 1952; Knott 1961; Gerechter-Amitai *et al.* 1971; Kerber and Dyck 1973). Green *et al.* (1960) pointed out that the most convincing evidence of a gene for rust resistance is the isolation of such a gene in a very susceptible variety. A number of alien stem rust resistance genes have been identified as listed in Table 1.

2.4.1 Table 1. List of Identified Alien Stem Rust (*Sr*) Resistance Genes

Sr Gene	Alien donor
*Sr*9d (*Sr*1)	*T. dicoccum* (Knott 1968; McIntosh 1973)
*Sr*2	*T. dicoccum* (Yaroslav emmer) (Ausemus *et al.* 1946; Knott 1968)
*Sr*3	*T. durum* (Ausemus *et al.* 1946; McIntosh 1973)
*Sr*4	*T. durum* (Iumillo durum) (Ausemus *et al.* 1946; McIntosh 1973)
*Sr*7b	*T. dicoccum* (Khapli emmer) (Knott 1966)
*Sr*9c (*SrTt*1)	*T. timopheevi* (McIntosh and Gyarfas 1971; McIntosh 1973)
*SrTt*2	*T. timopheevi* (McIntosh and Gyarfas 1971)
*Sr*11	*T. durum* (Gaza durum) (Watson and Stewart 1956; McIntosh 1973)
*Sr*17	*T. dicoccum* (Yaroslav emmer) (McIntosh *et al.* 1967; McIntosh 1973)
*Sr*21	*T. boeoticum* (Gerechter-Amitai *et al.* 1971; The 1973)
*Sr*22	*T. monococcum* (Kerber and Dyck 1973; The 1973)
*Sr*24	*A. elongatum* (Knott and Dvorak 1976)

(continued)

Table 1. List of Identified Alien Stem Rust (*Sr*) Resistance Genes (continued)

Sr Gene	Alien donor
*Sr*25	*A. elongatum* (Knott and Dvorak 1976)
*Sr*26	*A. elongatum* (Knott and Dvorak 1976)
*Sr*27	*S. cereale* (Imperial rye) (Luig and Watson 1976)

3. EXPERIMENTAL MATERIALS

3.1 Parental Lines Used

The varieties Glenlea, Wheat-Rye Translocation stock (WRT) ND71-13-1066, Line W (W3563) and W3498 were used in this study.

Glenlea is a spring utility wheat developed by the Plant Science Department, University of Manitoba, licensed in March 1972. It was derived from the cross (Pembina^2 X Bage) X CB100. CB100 is a Mexican strain having the cultivars Sonora 64, Tezanos Pintos Precoz and Nainari 60 in its parentage. It is resistant to all prevalent races of leaf and stem rust (Evans *et al.* 1972).

(WRT) ND71-13-1066 is a Wheat-Rye Translocation (WRT) stock with a portion of a rye chromosome from *S. cereale* cv Imperial in the genetic background of common wheat *T. aestivum* cv Thatcher (ND303*3//WRT238/5*Tc) obtained from the 1972 International Spring Wheat Rust Nursery plot #478. It is resistant to stem rust and carries the resistance gene Sr27 transferred by Acosta (1962) and developed and studied by A. Acosta-Carreon and E.R. Sears in the USDA Missouri Co-operative program at the Missouri Agricultural Experiment Station.

Line W (W3563) is an Australian cultivar produced by Gyarfas at Sydney University by selection from the cross W1906/ *T. timopheevi* W1899/2/3*Steinwedel W199. It is a stem rust resistant

line carrying the resistance gene SrTt2 (McIntosh and Gyarfas 1971).

W3498 is an Australian cultivar bred for susceptibility to strains of *P. graminis secalis* and highly susceptible to all strains of *P. graminis tritici* (Luig and Watson 1976).

3.2 Stem Rust Races Used

Pure cultures of stem rust races C25(38), C65(38), C49(15) and C33(15B-1L) were obtained from Dr. G.J. Green of Agriculture Canada Research Station, Winnipeg. These races were increased on adult Little Club plants in isolated greenhouse compartments of the Plant Science Department greenhouses. The purity of the races was tested on the differential hosts and the parental lines. Table 2 lists the races used and their virulence formulae. The effective resistance genes are given in the numerator while ineffective genes are those in the denominator.

TABLE 2. Stem Rust Race Number, Their Virulence Formulae, and Standard Race Equivalent

Race Number	Virulence Formulae	Standard Race
C25(38)	9a, 9e, Tt2 / 5, 6, 7a, 8, 10, 11, 15	38
C33(15B-1L)	6, 9a, 9b, 13, 15, 17, 22, Tt2 / 5, 7a, 8, 9d, 9e, 10, 11, 14	15B
C49(15)	6, 9a, 9b, 11, 13, 15, 17, 22, Tt2 / 5, 7a, 8, 9d, 10, 14	15
C65(38)	6, 8, 9e, 11, 17, Tt2 / 5, 7a, 9a, 10, 15	38

Differential cultivars: 5 = Sr5, 6 = Sr6, 7a = Sr7a, 8 = Sr8, 9a = Sr9a, 9b = Sr9b, 9d = Sr9d, 9e = Sr9e, 10 = Sr10, 11 = Sr11, Tt2 = SrTt2, 13 = Sr13, 14 = Sr14, 15 = Sr15, 17 = Sr17, 22 = Sr22.

Sources: Green (1976) Canadian Plant Disease Survey 1976.

3.3 Methods of Seedling Inoculation

Seedlings were inoculated at the first leaf stage by spraying with urediospores suspended in oil and then left for 30 minutes to dry. They were then transferred to incubation chambers, sprayed with water containing Tween-20 and then fogged with a fine spray of water and incubated for 24 hours at 60-65°F. During this time they were periodically fogged to maintain a saturated atmosphere. After 24 hours incubation, the pots were transferred to greenhouse benches where they remained until notes were taken on infection types 12 to 14 days after inoculation.

3.4 Recording Pathological Data

The classification of infection types on seedlings (Table 3) was in accordance with the system proposed by Stakman *et al.* (1962).

TABLE 3. Classes of Host Reaction and Types of Rust Infection

Symbol for infection type	Valuation in terms of pathogen-host reaction	Pathogen-host reaction abbreviation
0; ;1	Highly resistant	HR
1, 1+	Resistant	R
2, 2+, X	Moderately Resistant	MR
3, 3+, 4	Susceptible	S

0; = no uredia are developed, hypersensitive flecks occur.
1 = uredia are very small and surrounded by sharp, hypersensitive necrotic areas.
2 = the uredia are small to medium in size, hypersensitive areas present in the form of necrotic halos, surrounding green islands in the centre of which the uredia are usually located.
3 = uredia are of medium size and usually separate. Necrosis and hypersensitiveness are absent but chlorotic areas may surround the uredia, especially under unfavorable conditions.
4 = uredia are large and usually coalesce to form large irregular pustules.
X = plants are heterogeneous in their reaction.
The symbols -, ±, +, indicate quantitative variations in infection types.

Source: Stakman *et al.* (1962)

A B C D

Figure 1. Typical stem rust reactions on seedlings of W3498(A), Glenlea(B), Line W (W3563)(C) and (WRT) ND71-13-1066(D) inoculated with race C25(38)

4. EXPERIMENTAL PROCEDURE

4.1 Determination of the Nature and Number of Resistance Genes in the Parental Varieties Glenlea, Wheat-Rye-Translocation Stock (WRT) ND71-13-1066 and Line W (W3563)

In order to determine the number of stem rust resistance genes in each of the resistant parental varieties Glenlea, Wheat-rye-translocation stock (WRT) ND71-13-1066 and Line W (W3563), the three varieties were each crossed and backcrossed to the highly susceptible variety W3498 using it as a female and male parent, respectively. A large amount of F1 seed, F2 seed, together with F3 and BC1F2 families of Glenlea X W3498, (WRT) ND71-13-1066 X W3498, Line W (W3563) X W3498 crosses was obtained. Populations were inoculated with four test races, C25(38), C33(15B-1L), C49(15) and C65(38).

4.1.1 Handling F1 Seed

Sets of 10 to 20 F1 seeds from each of the crosses Glenlea X W3498, (WRT) ND71-13-1066 X W3498 and Line W (W3563) X W3498, together with the parental lines used, were grown in pots at the Agriculture Canada, Research Station, Winnipeg greenhouses and the seedlings were inoculated with each of the four stem rust races, C25(38), C33(15B-1L), C49(15) and C65(38) in order to determine whether resistance in Glenlea (WRT) ND71-13-1066 and Line W (W3563) to the four stem races is dominant or recessive. The seedlings were handled as described in sections

3.3 and 3.4.

4.1.2 Handling F2 Populations

Populations of 100 to 200 F2 plants from each of the crosses Glenlea X W3498, (WRT) ND71-13-1066 X W3498, Line W (W3563) X W3498, were tested with each of the races C25(38), C33(15B-1L), C49(15) and C65(38). Batches of 25 seeds were grown in pots together with the parental lines involved in the cross at the Agriculture Canada Research Station Winnipeg greenhouses. The seedlings were inoculated with pure cultures at the first leaf stage and treated as detailed in sections 3.3 and 3.4.

4.1.3 Handling F3 Families

Twenty-five seedlings from each F3 family from the Glenlea X W3498, (WRT) ND71-13-1066 X W3498 and Line W (W3563) X W3498 crosses were tested with each of the races C25(38), C33(15B-1L), C49(15) and C65(38). Individual F3 families were grown in each pot together with the parental varieties. The seedlings were inoculated with pure cultures at the first leaf stage and handled as described in sections 3.3 and 3.4.

4.1.4 Handling BC1F2 Families

Twenty-five seedlings from each backcross family from the Glenlea X $W3498^2$, (WRT) ND71-13-1066 X $W3498^2$, Line W (W3563) X $W3498^2$ backcrosses were tested with each of the races C25(38), C33(15B-1L), C49(15), C65(38). Individual BC1F2 families were grown in each pot at the Agriculture Canada Research Station

Winnipeg greenhouses together with the parental varieties involved in the crosses. The seedlings were inoculated with pure cultures at the first leaf stage and handled as described in sections 3.3 and 3.4.

4.2 Transfer of Stem Rust Resistance Gene Sr27 from the Wheat-Rye-Translocation Stock (WRT) ND71-13-1066 into Glenlea

The wheat-rye translocation stock (WRT) ND71-13-1066 known to possess the stem rust resistance gene Sr27 was crossed as a male parent to the variety Glenlea at the Department of Plant Science greenhouses. F1 seeds were grown singly in pots and backcrossed as female parents to Glenlea. BC1F1 seeds as well as F2 seeds were obtained. F1, F2 and BC1F1 seeds were space planted in the field at the Point during May-August 1976, from which F2, F3 and BC1F2 seeds were obtained. F1 seedlings, F2 populations, F3 and BC1F2 families were tested with stem rust races C25(38), C33(15B-1L), C49(15), C65(38) at the Agriculture Canada Research Station Winnipeg greenhouses. Race C25(38) which is relatively heavy on Glenlea (2 to 2+ infection type and 0; on WRT stock), was used as a test race in isolating resistant seedlings (0; infection type) from BC1F2 families which were then transplanted in pots and maintained at the Department of Plant Science greenhouses and backcrossed as female parents to Glenlea. A total of three backcrosses were made to the recurrent parent Glenlea, each time carrying over the resistant (0; infection type) seedlings.

4.2.1 Handling F1 Seeds, F2 Populations, F3 and BC1F2 Families

F1 seedlings, F2 populations, F3 and BC1F2 families were inoculated with pure cultures of stem rust races C25(38), C33(15B-1L), C49(15), C65(38) and handled as described in sections 3.3 and 3.4, respectively.

4.3 Transfer of Stem Rust Resistance Gene SrTt2 from the *Triticum timopheevi* Derivative Line W (W3563) into Glenlea

The common wheat-*T. timopheevi* derived Line W (W3563) carrying the stem rust resistance gene SrTt2, was crossed as a male parent to Glenlea at the Department of Plant Science greenhouses. F1 seeds were grown singly in pots and backcrossed as female parents to Glenlea. F1, F2 and BC1F1 seeds were space planted in the field at the Point during May-August 1976 from which F2 seeds, F3 and BC1F2 families were tested with stem rust races C25(38), C33(15B-1L), C49(15), C65(38) at the Agriculture Canada Research Station Winnipeg greenhouses. Race C25(38) which is relatively heavy on Glenlea [2 to 2+ reaction type and ;1 on Line W (W3563)] was used as a test race in isolating resistant seedlings from BC1F2 families which were then transplanted in pots and maintained at the Department of Plant Science greenhouses and backcrossed as female parents to Glenlea. A total of three backcrosses were made to Glenlea each time testing the seedlings with race C25(38) and carrying over the resistant (;1 infection type) seedlings.

4.3.1 Handling F1 Seeds, F2 Populations, F3 and BC1F2 Families

F1 seedlings, F2 populations, F3 and BC1F2 families were inoculated with pure cultures of stem rust races C25(38), C33(15B-1L), C49(15), C65(38) and handled as described in sections 3.3 and 3.4, respectively.

4.4 A Cross Between Wheat-Rye-Translocation Stock (WRT) ND71-13-1066 Carrying the Gene Sr27 and Line W (W3563) Carrying the Gene SrTt2

The two sources of stem rust resistance (WRT) ND71-13-1066 and the common wheat-*T. timopheevi* derivative Line W (W3563) were crossed at the Department of Plant Science greenhouses using (WRT) ND71-13-1066 as a male parent. F1 seeds were grown singly in pots from which F2 seeds were obtained. F1 and F2 seeds were space planted in the field at the Point during May-August 1976, from which F2 populations and F3 families were obtained.

4.4.1 Handling F1 Seeds, F2 Populations and F3 Families

F1 seedlings, F2 populations and F3 families were inoculated with pure cultures of stem rust races C25(38), C33(15B-1L), C49(15), C65(38) and handled as described in sections 3.3 and 3.4, respectively.

5. RESULTS AND DISCUSSION

5.1 Mode of Inheritance

The nature and number of resistance genes in Glenlea, Wheat-Rye-Translocation (WRT) stock ND71-13-1066 and line W (W3563) were determined by crossing and backcrossing each to the susceptible variety W3498. The parental lines, F1, F2, F3 and BC1F2 were tested with stem rust races C25(38), C65(38), C49(15) and C33(15B-1L). The seedling reactions of Glenlea, (WRT) ND71-13-1066, Line W (W3563) and W3498 are presented in Figure 1.

Glenlea X W3498

The seedling reaction of Glenlea, W3498 and the F1, F2, F3 and BC1F2 progeny of the cross between Glenlea and W3498 to race C25(38) are presented in Table 4. The F1 seedlings were susceptible [infection type (4)] like the susceptible parent W3498, indicating that resistance was inherited as a recessive trait. The F2 population segregated into the two parental infection types [type (2) and (4)] and were classified as either resistant or susceptible, according to the classification by Stakman *et al.* (1962) as indicated in Table 3. Forty-two seedlings were resistant and 120 seedlings were susceptible. This fitted satisfactorily the 1R:3S ratio (P = .75-.80) for one recessive gene. Twenty-one F3 lines were homozygous resistant infection type (2), 45 lines segregated for (2) and (4) infection types 278R:797S and 24 lines were homozygous susceptible [infection type (4)].

Thirty-two BC1F2 lines segregated for (2) and (4) infection types and 30 lines were homozygous susceptible. The observed segregations of both the F3 and BC1F2 lines were good fits to the expected 1R:2Seg:1S and 1Seg:1S ratios (P values of .90-.95 and .75-.80), respectively. It was concluded that Glenlea resistance to race C25(38) is conditioned by one recessive gene.

TABLE 4. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Glenlea/W3498 Inoculated with Race C25(38)

Generation or parent	Infection type or breeding behaviour*			Expected ratio	Chi-square	P-value
	R	Seg.	S			
Glenlea	2	-	-			
W3498	-	-	4			
F1	-	-	4			
F2	42	-	120	1:3	0.07407	.75-.80
F3	21	45	24	1:2:1	0.20000	.90-.95
BC1F2		32	30	1:1	0.064516	.75-.80

*R = Resistant; Seg. = Segregating; S = Susceptible

With the F3 and BC1F2 segregating lines segregation was:
45 F3 lines segregated 278R:797S, P = .50-.70 for a 1:3 ratio
32 BC1F2 lines segregated 205R:570S, P = .30-.50 for a 1:3 ratio

Seedling reactions to race C65(38) are presented in Table 5. The F1 seedlings were susceptible indicating that resistance in Glenlea was governed by a recessive gene. The F2 population segregated 46R:154S. This fitted satisfactorily the 1R:3S ratio (P = .70-.75)

for one recessive gene. The F3 and BC1F2 lines that were resistant, susceptible or segregated to race C25(38) were also resistant, susceptible or segregated to race C65(38) as shown in Table 5, indicating that the recessive gene was also effective against race C65(38).

TABLE 5. Stem Rust Reactions of F1, F2, F3 and BC1F2 of the Cross Glenlea/W3498 Inoculated with Race C65(38)

Generation or parent	Infection type or breeding behaviour*			Expected ratio	Chi-square	P-value
	R	Seg.	S			
Glenlea	2	-	-			
W3498	-	-	4			
F1	-	-	4			
F2	46	-	154	1:3	0.426667	.70-.75
F3	21	45	24	1:2:1	0.20000	.90-.95
BC1F2		32	30	1:1	0.064516	.75-.80

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 and BC1F2 segregating lines segregation was:
45 F3 lines segregated 275R:775S, P = .30-.50 for a 1:3 ratio
32 BC1F2 lines segregated 205R:563S, P = .25-.30 for a 1:3 ratio

In tests with race C49(15) (Table 6), the F1 seedlings were susceptible [type (4) infection] like the susceptible parent W3498. The F2 population segregated 45R:150S which is a good fit (P = .50-.70) to the 1R:3S ratio for one recessive gene. The F3 and BC1F2 lines that were resistant, susceptible or segregated to races C25(38) and

C65(38) were also resistant, susceptible or segregated to race C49(15) conforming to a one recessive gene segregation as shown in Table 6.

TABLE 6. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Glenlea/W3498 Inoculated with Race C49(15)

Generation or parent	Infection type or breeding behaviour*			Expected ratio	Chi-square	P-value
	R	Seg.	S			
Glenlea	2	-	-			
W3498	-	-	4			
F1	-	-	4			
F2	45	-	150	1:3	0.384615	.50-.70
F3	21	45	24	1:2:1	0.20000	.90-.95
BC1F2		32	30	1:1	0.064516	.75-.80

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 and BC1F2 segregating lines segregation was:
45 F3 lines segregated 285R:815S, P = .30-.50 for a 1:3 ratio
32 BC1F2 lines segregated 211R:589S, P = .30-.50 for a 1:3 ratio

In tests with race C33(15B-1L) (Table 7), the F1 seedlings were susceptible like the susceptible parent W3498, indicating that resistance in Glenlea was conditioned by a recessive gene. The F2 population segregated 27R:97S. This fitted satisfactorily the postulated 1R:3S ratio (P - .30-.50) for one recessive gene. The F3 and BC1F2 lines segregated as for races C25(38), C65(38) and C49 conforming to the 1R:2Seg:1S (P = .90-.95) and 1Seg:1S (P = .75-.80) ratios, respectively, for one recessive gene. Therefore, resistance

to race C33(15B-1L) was governed by one recessive gene, and that the recessive gene in Glenlea was effective against all four stem rust races used.

TABLE 7. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Glenlea/W3498 Inoculated with Race C33(15B-1L)

Generation or parent	Infection type or breeding behaviour*			Expected ratio	Chi-square	P-value
	R	Seg.	S			
Glenlea	2	-	-			
W3498	-	-	4			
F1	-	-	4			
F2	27	-	97	1:3	0.68817	.30-.50
F3	21	45	24	1:2:1	0.20000	.90-.95
BC1F2		32	30	1:1	0.064516	.75-.80

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 and BC1F2 segregating lines segregation was:
45 F3 lines segregated 290R:812S, P = .30-.50 for a 1:3 ratio
32 BC1F2 lines segregated 210R:580S, P = .30-.50 for a 1:3 ratio

(WRT) ND71-13-1066 X W3498

The seedling reaction of (WRT) ND71-13-1066, W3498 and the F1, F2, F3 and BC1F2 generations to race C25(38) are presented in Table 8. The F1 seedlings were resistant (0;) like the resistant parent (WRT) ND71-13-1066, indicating that resistance was dominant. The F2 population segregated into three infection types: 161 flecks, 52 type (2) and 16 type (4) infection. This fitted satisfactorily the postulated 12:3:1 ratio with a P value of .20-.25 for two dominant genes; one epistatic to the other. The 65 F3 lines segregated: 32 lines were resistant, 30 lines segregated and 3 lines were homozygous susceptible which was a good fit (P = .50-.70) to the 7R:8Seg:1S ratio for two dominant genes. Within the resistant lines, 3 lines segregated for (0;) and (2) infection types and 29 lines were homozygous resistant [(0;) or (2) infection type]. Within the segregating F3 lines, 17 lines segregated for (0;), (2) and (4) infection types [400R(326(0;):74(2)]:22S, 7 lines segregated for (0;) and (4) infection types 96R:29S and 6 lines segregated for (2) and (4) infection types 93R:37S. Under a two dominant gene hypothesis, 20 lines should be homozygous resistant (0;), 4 lines should be homozygous resistant (2), 4 lines should be resistant [segregating for (0;) and (2)], 16 lines should segregate for (0;), (2) and (4) infection types, 8 lines should segregate for (0;) and (4) and 8 lines should segregate for (2) and (4) infection types. The observed segregation of the F3 lines confirmed the two gene hypothesis as indicated in Table 8. The 52 BC1F2 lines had 41 lines segregating and 11 lines homozygous susceptible. Within the segregating BC1F2

14 lines segregated for (2) and (4) infection types 243R:93S, 12 lines segregated for (0;), (2) and (4) infection types [278R(228(0;): 50(2)]:22S and 15 lines segregated for (0;) and (4) infection types 274R:86S. This fitted satisfactorily (P = .50-.70) the postulated 3Seg:1S ratio (Table 8). Under a two dominant gene hypothesis, 13 lines should segregate for (0;), (2) and (4) infection types, 13 lines should segregate for (0;) and (4), 13 lines should segregate for (2) and (4) infection types and 13 lines should be homozygous susceptible [type (4) infection]. The segregation of the 52 lines conformed to the expected segregation, further confirming that two dominant genes condition seedling resistance of (WRT) ND71-13-1066 to race C25(38). One gene confers a fleck infection type, while the second gene conditions a type (2) infection, and that the fleck gene is epistatic to the (2) type gene.

TABLE 8. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross (WRT) ND71-13-1066/W3498 Inoculated with Race C25(38)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
(WRT) ND71-13-1066	0;	-	-			
W3498	-	-	4			
F1	0;	-	-			
F2	161(0;):52(2)	-	16	12:3:1	2.784571	.20-.25
F3	32	30	3	7:8:1	0.916484	.50-.70
BC1F2		41	11	3:1	0.410256	.50-.70

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:
17 lines segregated 326(0;):74(2):22(4), P = .50-.70 for a 12:3:1 ratio
7 lines segregated 96(0;):29(4) , P = .50-.70 for a 3:1 ratio
6 lines segregated 93(2) :37(4) , P = .30-.50 for a 3:1 ratio

Within the BC1F2 segregating lines segregation was:
12 lines segregated 228(0;):50(2):22(4), P = .50-.70 for a 12:3:1 ratio
15 lines segregated 274(0;):86(4) , P = .50-.70 for a 3:1 ratio
14 lines segregated 243(2) :93(4) , P = .25-.30 for a 3:1 ratio

In tests with race C65(38), (Table 9) the F1 seedlings were resistant [(0;) infection type] like the resistant parent (WRT) ND71-13-1066, indicating that resistance was dominant. The F2 population segregated into three groups: 105 flecks, 32 type (2) and 12 type (4) infection. This fitted well the postulated 12:3:1 ratio with a P value of .30-.50, indicating that two dominant genes govern rust reaction to race C65(38), one gene epistatic to the other. The

F3 and BC1F2 lines that were resistant, susceptible or segregated to race C25(38) were also resistant, susceptible or segregated to race C65(38) as shown in Table 9, indicating that the two genes were effective against both races. One of the genes conditions a fleck (0;) infection type while the second gene conditions a type (2) infection.

TABLE 9. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross (WRT) ND71-13-1066/W3498 Inoculated with Race C65(38)

Generation or parent	Infection type or breeeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
(WRT) ND71-13-1066	0;	-	-			
W3498	-	-	4			
F1	0;	-	-			
F2	105(0;):32(2)	-	12	12:3:1	1.773049	.30-.50
F3	32	30	3	7:8:1	0.916484	.50-.70
BC1F2		41	11	3:1	0.410256	.50-.70

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:
17 lines segregated 311(0;):85(2):22(4), P = .50-.70 for a 12:3:1 ratio
7 lines segregated 121(0;):47(4) , P = .30-.50 for a 3:1 ratio
6 lines segregated 109(2) :35(4) , P = .80-.90 for a 3:1 ratio

Within the BC1F2 segregating lines segregation was:
12 lines segregated 231(0;):49(2):20(4), P = .50-.70 for a 12:3:1 ratio
15 lines segregated 278(0;):97(4) , P = .70-.75 for a 3:1 ratio
14 lines segregated 251(2): 94(4) , P = .30-.50 for a 3:1 ratio

In tests with race C49(15) (Table 10), the F1 seedlings were resistant [(0;) infection type] like the resistant parent (WRT) ND71-13-1066. The F2 population segregated into three groups: 94 flecks, 34 type (2), 10 type (4) infection. This fitted satisfactorily the 12:3:1 ratio with a P value of .10-.20 indicating that two dominant genes govern rust reaction to race C49(15). The segregation distribution of F3 and BC1F2 lines was as for races C25(38) and C65(38) as indicated in Table 10.

TABLE 10. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross (WRT) ND71-13-1066/W3498 Inoculated with Race C49(15)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
(WRT) ND71-13-1066	0;	-	-			
W3498	-	-	4			
F1	0;	-	-			
F2	94(0;):34(2)	-	10	12:3:1	3.642512	.10-.20
F3	32	30	3	7:8:1	0.916484	.50-.70
BC1F2		41	11	3:1	0.410256	.50-.70

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:
17 lines segregated 325(0;):76(2):24(4), P = .75-.80 for a 12:3:1 ratio
7 lines segregated 124(0;):46(4), P = .50-.70 for a 3:1 ratio
6 lines segregated 117(2) :33(4), P = .30-.50 for a 3:1 ratio

Within the BC1F2 segregating lines segregation was:
12 lines segregated 219(0;):51(2):16(4), P = .80-.90 for a 12:3:1 ratio
15 lines segregated 273(0;):97(4), P = .50-.70 for a 3:1 ratio
14 lines segregated 270(2) :78(4), P = .25-.30 for a 3:1 ratio

In tests with race C33(15B-1L) (Table 11), the F1 seedlings were similar in reaction to the resistant parent (WRT) ND71-13-1066 [(0;) infection type]. This indicated that the gene(s) that conditioned resistance in ND71-13-1066 to race C33(15B-1L) was dominant. The F2 population segregated into three groups: 114 seedlings had flecks, 52 seedlings had type (2) infection and 13 seedlings had a type (4) infection. This fitted satisfactorily a 15:1 ratio with a P value of .50-.70 for two dominant genes; one epistatic to the other. The F3 and BC1F2 lines that were resistant, susceptible or segregated to races C25(38), C65(38) and C49(15) were also resistant or susceptible or segregated to race C33(15B-1L) as shown in Table 11, indicating that the same genes were effective against all four stem rust races used.

TABLE 11. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross (WRT) ND71-13-1066/W3498 Inoculated with Race C33(15B-1L)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
(WRT) ND71-13-1066	0;	-	-			
W3498	-	-	4			
F1	0;	-	-			
F2	114(0;):52(2)	-	13	12:3:1 15:1	13.4767 0.31322	<.001 .50-.70
F3	32	30	3	7:8:1	0.916484	.50-.70
BC1F2		41	11	3:1	0.410256	.50-.70

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:
17 lines segregated 290(0;):80(2):21(4), P = .50-.70 for a 12:3:1 ratio
7 lines segregated 125(0;):36(4) , P = .30-.50 for a 3:1 ratio
6 lines segregated 104(2) :34(4) , P = .90-.95 for a 3:1 ratio

Within the BC1F2 segregating lines segregation was:
12 lines segregated 215(0;):59(2):21(4), P = .50-.70 for a 12:3:1 ratio
15 lines segregated 267(0;):21(4) , P = .50-.70 for a 3:1 ratio
14 lines segregated 254(2) :96(4) , P = .25-.30 for a 3:1 ratio

Line W (W3563) X W3498

The seedling reaction of Line W (W3563), W3498, F1, F2 F3 and BC1F2 to race C25(38) are presented in Table 12. The F1 seedlings were resistant [(;1) infection type], indicating that the gene in Line W (W3563) is dominant. The F2 population segregated into the two parental types [(;1) and (4)]. Seventy-six seedlings were resistant [(;1) infection type] and 26 were susceptible [type (4) infection]. This fitted satisfactorily the 3:1 ratio (P = .75-.80) for one dominant gene. The F3 lines segregated into 15 homozygous resistant [(;1) infection type], 37 segregated for (;1) and (4) infection types and 19 were homozygous susceptible. This was a good fit (P = .70-.75) to the 1:2:1 ratio for one dominant gene. The 62 BC1F2 lines had 28 lines segregating for (;1) and (4) infection types (Table 12) and 34 lines were homozygous susceptible which was a good fit (P = .30-.50) to the 1Seg:1S ratio for one dominant gene.

Within the segregating F3 lines, the 37 lines segregated 661R:239S; this was a good fit to the 3R:1S ratio for one dominant gene. The 28 BC1F2 segregating lines segregated into 512R:188S, further confirming the one gene hypothesis.

TABLE 12. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Line W (W3563)/W3498 Inoculated with Race C25(38)

Generation or parent	Infection type or breeding behaviour*			Expected ratio	Chi-square	P-value
	R	Seg.	S			
Line W (W3563)	;1	-	-			
W3498	-		4			
F1	;1	-	-			
F2	76	-	26	3:1	0.051282	.75-.80
F3	15	37	19	1:2:1	0.57746	.70-.75
BC1F2		28	34	1:1	0.580645	.30-.50

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 and BC1F2 segregating lines segregation was:
37 F3 lines segregated 661R:239S, P = .25-.30 for a 3:1 ratio
28 BC1F2 lines segregated 512R:188S, P = .25-.30 for a 3:1 ratio

In tests with race C65(38), F1 seedlings were similar in reaction [(;1) reaction] to the resistant parent Line W (W3563) (Table 13), indicating that resistance in Line W (W3563) was conditioned by a dominant gene. The F2 population segregated into the two parental types [(;1) and (4) infection types]; 105 seedlings were resistant (;1) and 41 seedlings were susceptible [type (4) infection]. This fitted satisfactorily the 3:1 ratio with a P value of .30-.50 for one dominant gene. F3 and BC1F2 lines that were resistant, susceptible or segregated to race C25(38) were also resistant, susceptible or segregated when tested with race C65(38) indicating that

the same gene was effective against race C65(38) as indicated in Table 13. The 37 F3 segregating lines segregated 643R:231S [(;1) and (4) infection types]. The 28 BC1F2 lines segregated 496R:179S [(;1) and (4) infection types], conforming to the one dominant gene hypothesis.

TABLE 13. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Line W (W3563)/W3498 Inoculated with Race C65(38)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Line W (W3563)	;1	-	-			
W3498	-	-	4			
F1	;1	-	-			
F2	105	-	41	3:1	0.739726	.30-.50
F3	15	37	19	1:2:1	0.57746	.70-.75
BC1F2		28	34	1:1	0.580645	.30-.50

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 and BC1F2 segregating lines segregation was:
37 F3 lines segregated 643R:231S, P = .30-.50 for a 3:1 ratio
28 BC1F2 lines segregated 496R:179S, P = .30-.50 for a 3:1 ratio

With race C49(15) (Table 14), F1 seedlings were resistant [(;1) reaction] like Line W (W3563), indicating that the gene conditioning resistance to race C49(15) was dominant. The F2 population segregated 55 resistant [(;1) infection type] and 19 seedlings were susceptible [type (4) infection]. This fitted satisfactorily (P =

.80-.90) the 3:1 ratio for one dominant gene. The segregation distribution of F3 and BC1F2 lines were as for races C25(38) and C65(38) as shown in Table 14. The segregating lines segregated for one gene.

TABLE 14. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Line W (W3563)/W3498 Inoculated with Race C49(15)

Generation or parent	Infection type or breeding behaviour*			Expected ratio	Chi-square	P-value
	R	Seg.	S			
Line W (W3563)	;1	-	-			
W3498	-	-	4			
F1	;1	-	-			
F2	55	-	19	3:1	0.0180180	.80-.90
F3	15	37	19	1:2:1	0.57746	.70-.75
BC1F2		28	34	1:1	0.580645	.30-.50

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 and BC1F2 segregating lines segregation was:
37 F3 lines segregated 672R:243S, P = .25-.30 for a 3:1 ratio
28 BC1F2 lines segregated 490R:180S, P = .25-.30 for a 3:1 ratio

In tests with race C33(15B-1L) (Table 15), F1 seedlings were resistant (;1) like the resistant parental Line W (W3563) indicating that resistance was dominant. The F2 population segregated into the two parental infection types [(;1) and (4)]; 67 seedlings were resistant (;1) and 24 seedlings were susceptible [type (4) infection].

This is a good fit (P = .75-.80) to the 3:1 ratio for one dominant gene. The F3 and BC1F2 lines that were resistant or susceptible or segregated to races C25(38), C65(38), C49(15) were also resistant, susceptible or segregated when tested with race C33(15B-1L) (Table 15) indicating that the same gene was effective against all four stem rust races.

TABLE 15. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Line W (W3563)/W3498 Inoculated with Race C33(15B-1L)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Line W (W3563)	;1	-	-			
W3498	-	-	4			
F1	;1	-	-			
F2	67	-	24	3:1	0.091575	.75-.80
F3	15	37	19	1:2:1	0.57746	.70-.75
BC1F2		28	34	1:1	0.580645	.30-.50

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 and BC1F2 segregating lines segregation was:
37 F3 lines segregated 683R:242S, P = .30-.50 for a 3:1 ratio
28 BC1F2 lines segregated 501R:184S, P = .25-.30 for a 3:1 ratio

Glenlea X (WRT) ND71-13-1066

The seedling reactions of parental lines, F1, F2, F3 and BC1F2 of the cross between Glenlea and (WRT) ND71-13-1066 to race C25(38) are presented in Table 16. The F1 seedlings were resistant [(0;) infection type] like (WRT) ND71-13-1066, indicating that the gene in (WRT) ND71-13-1066 is dominant and epistatic to the gene in Glenlea. The F2 population segregated: 182 seedlings had flecks (0;), 71 seedlings had type (2) infection and 9 seedlings had type (4) infection. This fitted the postulated 48:13:3 ratio (P = .025-.05) for a three gene difference between the two cultivars; two dominant and one recessive. Sixty-nine F3 lines were also tested. Thirty seven lines were resistant [(0;) or (2) infection type], 30 lines segregated and 2 lines were homozygous susceptible infection type (4). This distribution fitted well the 37R:26Seg:1S ratio (P = .50-.70) for a three gene difference between the two cultivars. Within the resistant lines, 16 lines segregated for (0;) and (2) infection types. The distribution of the 30 segregating lines was: 19 lines segregated for (0;), (2) and (4) infection types, 1 line segregated for (0;) and (4) infection types and 10 lines segregated for (2) and (4) infection types. Under the three gene hypothesis, two dominant and one recessive, the F3 lines should segregate: 40 lines should be resistant, 28 segregating and 1 susceptible. Within the segregating lines, 9 lines should segregate for (0;), (2) and (4) in a 48:13:3 ratio, 4 lines should segregate for (0;), (2), (4), in a 12:3:1 ratio, 4 lines should segregate for (0;), (2), (4) in a 12:1:3 ratio, 2 lines should segregate for (0;) and (4) in a 3:1 ratio, 2 lines should segregate

for (2) and (4) in a 3:1 ratio, 2 lines should segregate for (2) and (4) in a 1:3 ratio and 4 lines should segregate for (2) and (4) in a 13:3 ratio. The observed segregation of the F3 lines conformed to the expected segregation as indicated in Table 16.

Of the 61 BC1F2 lines tested, 32 lines were resistant and 29 lines segregated. This was a good fit to the 1R:1Seg ratio (P = .70-.80) for a three gene difference between the two cultivars; two dominant and one recessive. Within the resistant lines, 19 lines segregated for (0;) and (2) infection type and 13 lines had type (2) infection. Within the segregating 29 lines, 8 lines segregated for (0;), (2) and (4) in a 48:13:3 ratio, 8 lines segregated for (0), (2) and (4) in a 12:1:3 ratio, 7 lines segregated for (2) and (4) in a 13:3 ratio and 6 lines segregated for (2) and (4) in a 1:3 ratio, confirming the three gene hypothesis. The three genes condition a fleck (0;), type (2) and type (2) infection, respectively. (WRT) ND71-13-1066 contains two dominant genes which confer a (0;) and (2) infection type, while Glenlea possesses a recessive gene that conditions a (2) infection type to race C25(38). It was, however, not possible to differentiate infection type (2) originating from these two sources.

TABLE 16. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Glenlea/(WRT) ND71-13-1066 Inoculated with Race C25(38)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Glenlea	2	-	-			
(WRT) ND71-13-1066	0;	-	-			
F1	0;	-	-			
F2	182(0;):71(2)		9	48:13:3 61:3	7.8876 0.9198	.025-.05 .30-.50
F3	37	30	2	37:26:1	1.1360	.50-.70
BC1F2	32	29		1:1	0.1475	.70-.80

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:

12 lines segregated 227(0;):62(2):11(4), P = .70-.75 for a 48:13:3 ratio
4 lines segregated 81(0;):15(2): 4(4), P = .30-.50 for a 12: 3:1 ratio
3 lines segregated 59(0;): 4(2):12(4), P = .75-.80 for a 12: 1:3 ratio
1 line segregated 21(0;): 4(4) , P = .25-.30 for a 3:1 ratio
4 lines segregated 76(2):20(4) , P = .30-.50 for a 3:1 ratio
3 lines segregated 16(2):59(4) , P = .30-.50 for a 1:3 ratio
3 lines segregated 64(2):11(4) , P = .30-.50 for a 13:3 ratio

Within the BC1F2 segregating lines segregation was:

8 lines segregated 132(0;):42(2):10(4), P = .50-.70 for a 48:13:3 ratio
7 lines segregated 138(2):37(4) , P = .30-.50 for a 13:3 ratio
8 lines segregated 155(0;):8(2):29(4) , P = .10-.20 for a 12: 1:3 ratio
6 lines segregated 34(2):92(4) , P = .50-.70 for a 1:3 ratio

In tests with race C65(38) (Table 17), the F1 seedlings were resistant (0;) like (WRT) ND71-13-1066, indicating that the gene in (WRT) ND71-13-1066 is dominant and epistatic to the gene in Glenlea. The F2 population segregated: 81 seedlings had flecks, 27 seedlings had infection type (2) and 7 seedlings had infection type (4). This fitted satisfactorily the postulated 48:13:3 ratio (P = .50-.70) for a three gene difference between the two cultivars; two dominant and one recessive. The F3 and BC1F2 lines that were resistant, susceptible or segregated to race C25(38) were also resistant, susceptible or segregated to race C65(38) conforming to the 37R:26Seg: 1S and 1R:1Seg ratio (P = .50-.70 and .70-.80), respectively, as shown in Table 17.

TABLE 17. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Glenlea/(WRT) ND71-13-1066 Inoculated with Race C65(38)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Glenlea	2	-	-			
(WRT) ND71-13-1066	0;	-	-			
F1	0;	-	-			
F2	81(0;):27(2)		7	48:13:3	1.3674	.50-.70
F3	37	30	2	37:26:1	1.1360	.50-.70
BC1F2	32	29		1:1	0.1475	.70-.80

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:

12 lines segregated 223(0;):68(2):9(4), P = .25-.30 for a 48:13:3 ratio
4 lines segregated 82(0;):13(2):5(4), P = .25-.30 for a 12: 3:1 ratio
3 lines segregated 53(0;):6(2):15(4), P = .70-.75 for a 12: 1:3 ratio
1 line segregated 18(0;):7(4) , P = .70-.75 for a 3: 1 ratio
4 lines segregated 72(2):28(4) , P = .30-.50 for a 3: 1 ratio
3 lines segregated 21(2):54(4) , P = .50-.70 for a 1: 3 ratio
3 lines segregated 63(2):9(4) , P = .10-.20 for a 13: 3 ratio

Within the BC1F2 segregating lines segregation was:

8 lines segregated 152(0;):36(2):12(4), P = .50-.70 for a 48:13:3 ratio
7 lines segregated 140(2):35(4) , P = .50-.70 for a 13: 1 ratio
8 lines segregated 147(0;):38(2):15(4), P = .10-.20 for a 12: 3:1 ratio
6 lines segregated 41(2):109(4) , P = .50-.70 for a 1: 3 ratio

In tests with race C49(15) (Table 18), the F1 seedlings were resistant (0;) like (WRT) ND71-13-1066, indicating that the gene in (WRT) ND71-13-1066 is dominant and epistatic to the gene in Glenlea. The F2 population segregated: 128 seedlings had flecks (0;), 36 seedlings had infection type (2) and 6 seedlings had infection type (4). This was a good fit to the expected 48:13:3 ratio (P = .75-.80) for a three gene difference between the two cultivars. The F3 and BC1F2 lines segregated for three genes as for races C25(38) and C65(38) as shown in Table 18.

TABLE 18. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Glenlea/(WRT) ND71-13-1066 Inoculated with Race C49(15)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Glenlea	2	-	-			
(WRT) ND71-13-1066	0;	-	-			
F1	0;	-	-			
F2	128(0;):36(2)		6	48:13:3	.5508	.75-.80
F3	37	30	2	37:26:1	1.1360	.50-.70
BC1F2	32	29		1:1	0.1475	.70-.80

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:

12 lines segregated 236(0;):49(2):10(4), P = .10-.20 for a 48:13:3 ratio
4 lines segregated 74(0;):16(2): 8(4), P = .50-.70 for a 12: 3:1 ratio
3 lines segregated 58(0;): 5(2):11(4), P = .50-.70 for a 12: 1:3 ratio
1 line segregated 19(0;):5(4) , P = .50-.70 for a 3: 1 ratio
4 lines segregated 77(2):21(4) , P = .30-.50 for a 3: 1 ratio
3 lines segregated 15(2):57(4) , P = .30-.50 for a 1: 3 ratio
3 lines segregated 63(2):12(4) , P = .50-.70 for a 13: 3 ratio

Within the BC1F2 segregating lines segregation was:

8 lines segregated 141(0;):44(2):7(4), P = .50-.70 for a 48:13:3 ratio
7 lines segregated 147(2):28(4) , P = .30-.50 for a 13: 3 ratio
8 lines segregated 150(0;):33(2):15(4), P = .30-.50 for a 12: 3:1 ratio
6 lines segregated 42(2):106(4) , P = .30-.50 for a 1: 3 ratio

In tests with race C33(15B-1L) (Table 19), the F1 seedlings were resistant (0;) like (WRT) ND71-13-1066 indicating that the gene in (WRT) ND71-13-1066 is dominant and epistatic to the gene in Glenlea. The F2 population segregated: 116 seedlings had flecks (0;), 39 seedlings had infection type (2) and 9 seedlings had infection type (4). This fitted satisfactorily the expected 48:13:3 ratio (P = .30-.50) for a three gene difference between the two cultivars; two dominant and one recessive. The F3 and BC1F2 lines that were resistant, susceptible or segregated to races C25(38), C65(38) and C49(15) were also resistant, susceptible or segregated to race C33(15B-1L) and their segregation conformed to the three gene hypothesis as indicated in Table 19. This indicates that the three resistance genes involved were effective on all four races used.

TABLE 19. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Glenlea/(WRT) ND71-13-1066 Inoculated with Race C33(15B-1L)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Glenlea	2	-	-			
(WRT) ND71-13-1066	0;	-	-			
F1	0;	-	-			
F2	116(0;):39(2)		9	48:13:3	1.5935	.30-.50
F3	37	30	2	37:26:1	1.1360	.50-.70
BC1F2	32	29		1:1	0.1475	.70-.80

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:

12 lines segregated 228(0;):57(2):12(4), P = .70-.75 for a 48:13:3 ratio
4 lines segregated 76(0;):15(2): 5(4), P = .50-.70 for a 12: 3:1 ratio
3 lines segregated 56(0;): 3(2):16(4), P = .50-.70 for a 12: 1:3 ratio
1 line segregated 20(0;): 5(4) , P = .50-.70 for a 3: 1 ratio
4 lines segregated 75(2):20(4) , P = .30-.50 for a 3: 1 ratio
3 lines segregated 17(2):58(4) , P = .50-.70 for a 1: 3 ratio
3 lines segregated 55(2):15(4) , P = .50-.70 for a 13: 3 ratio

Within the BC1F2 segregating lines segregation was:

8 lines segregated 147(0;):31(2):6(4), P = .25-.30 for a 48:13:3 ratio
7 lines segregated 145(2):27(4) , P = .30-.50 for a 13: 3 ratio
8 lines segregated 159(0;):32(2):9(4), P = .30-.50 for a 12: 3:1 ratio
6 lines segregated 40(2):105(4) , P = .30-.50 for a 1: 3 ratio

Glenlea X Line W (W3563)

The seedling reaction of Glenlea, Line W (W3563), F1, F2 and BC1F2 to race C25(38) are presented in Table 20. The F1 seedlings were resistant [(;1) infection type] like Line W (W3563), indicating that the gene in Line W (W3563) is dominant and epistatic to the gene in Glenlea. The F2 population segregated: 109 seedlings had (;1) infection type, 13 seedlings had (2) infection type and 23 seedlings had infection type (4). This was a good fit to the 12:1:3 ratio (P = .30-.50) for a two gene difference between the two cultivars; one dominant (;1) and one recessive [type (2) infection]. The breeding behaviour of the F3 lines confirmed the two gene hypothesis. Twenty-four lines were resistant, 28 lines segregated and 4 lines were homozygous susceptible. This fitted satisfactorily the expected 6R:9Seg:1S ratio (P = .50-.70) for a two gene difference between the two cultivars. Within the resistant lines, 15 were homozygous resistant [(;1) or (2) infection type], 9 lines segregated for (;1) and (2) infection types. The distribution of the 28 segregating lines was: 15 lines segregated for (;1), (2) and (4) infection types 312R[(293(;1):19(2)]:63S, 7 lines segregated for (;1) and (4) infection types 136R:39S and 6 lines segregated for (2) and (4) infection types 38R:94S, further confirming the two gene hypothesis; one dominant and one recessive as indicated in Table 20.

Forty-one BC1F2 lines were also tested. Twenty-three lines were resistant; 18 lines segregated. This was a good fit to the expected 1R:1Seg ratio (P = .30-.50) for a two gene difference between the two cultivars. Within the resistant lines, 8 were homozygous

resistant [(2) infection type] and 15 lines segregated for (;1) and (2) infection types. Within the segregating lines, 10 lines segregated for (;1), (2) and (4) infection types 207R[193(;1):14(2)] :41S and 8 lines segregated for (2) and (4) infection types 53R:147S. Under the two gene hypothesis 21 BC1F2 lines were expected to be resistant and 21 lines segregating. The observed segregation of BC1F2 lines was a close fit to the expected for two genes; one dominant and one recessive. The dominant gene confers a (;1) infection type and the recessive gene confers a type (2) infection.

TABLE 20. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Glenlea/Line W (W3563) Inoculated with Race C25(38)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Glenlea	2	-	-			
Line W (W3563)	;1	-	-			
F1	;1					
F2	109(;1):13(2)	-	23	12:1:3	2.3564	.30-.50
F3	24	28	4	6:9:1	0.8889	.50-.70
BC1F2	23	18		1:1	0.6098	.30-.50

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:
15 lines segregated 312R[293(;1):19(2)] :63S, P = .30-.50 for a 12:1:3 ratio
7 lines segregated 136R:39S , P = .30-.50 for a 3:1 ratio
6 lines segregated 38R:94S , P = .30-.50 for a 1:3 ratio

Within the BC1F2 segregating lines segregation was:
10 lines segregated 207 193(;1):14(2) :41S, P = .50-.70 for a 12:1:3 ratio
8 lines segregated 53R:147S , P = .50-.70 for a 1:3 ratio

In tests with race C65(38) (Table 21), the F1 seedlings were resistant [(0;) infection type] like Line W (W3563). The F2 population segregated: 97 seedlings had (;1), 5 seedlings had (2) and 8 seedlings had type (4) infection. This is a good fit (P = .30-.50) to the expected 12:1:3 ratio, indicating that the two cultivars differed by two genes; one dominant and one recessive. The F3 and BC1F2 lines segregated as for race C25(38) conforming to the 6R:9Seg:1S and 1R:1Seg ratios for a two gene hypothesis as shown in Table 21.

TABLE 21. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Glenlea/Line W (W3563) Inoculated with Race C65(38)

Generation or parent	Infection type or breeding behaviour*			Expected ratio	Chi-square	P-value
	R	Seg.	S			
Glenlea	2	-	-			
Line W (W3563)	;1	-	-			
F1	;1	-				
F2	97(;1):5(2)	-	18	12:1:3	2.2888	.30-.50
F3	24	28	4	6:9:1	0.8889	.50-.70
BC1F2	23	18		1:1	0.6098	.30-.50

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:
15 lines segregated 274R[247(;1):25(2)]:56S, P = .30-.50 for a 12:1:3 ratio
7 lines segregated 132R:38S , P = .30-.50 for a 3:1 ratio
6 lines segregated 35R:115S , P = .30-.50 for a 1:3 ratio

Within the BC1F2 segregating lines segregation was:
10 lines segregated 201R[183(;1):18(2)]:39S, P = .50-.70 for a 12:1:3 ratio
8 lines segregated 53R:143S , P = .30-.50 for a 1:3 ratio

In tests with race C49(15) (Table 22), the F1 seedlings were resistant [(;1) infection type] like Line W (W3563). The F2 population segregated: 78 seedlings had (;1) infection type, 10 seedlings had tyoe (2) infection and 16 seedlings had type (4) infection. This is a good fit to the expected 12:1:3 ratio (P = .25-.30) for two genes difference between the two cultivars; one dominant and one recessive. The F3 and BC1F2 lines that were resistant, susceptible or segregated to races C25(38) and C65(38) behaved similarly to race C49(15) conforming to the two gene hypothesis as shown in Table 22. This indicated that the same genes were effective against races C25(38), C65(38) and C49(15).

TABLE 22. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Glenlea/Line W (W3563) Inoculated with Race C49(15)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Glenlea	2	-	-			
Line W (W3563)	;1	-	-			
F1	;1	-	-			
F2	78(;1):10(2)		16	12:1:3	2.5128	.25-.30
F3	24	28	4	6:9:1	0.8889	.50-.70
BC1F2	23	18		1:1	0.6098	.30-.50

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:
15 lines segregated 312R[290(;1):22(2)]:64S, P = .50-.70 for a 12:1:3 ratio
7 lines segregated 135R:40S , P = .50-.70 for a 3:1 ratio
6 lines segregated 37R:95S , P = .30-.50 for a 1:3 ratio

Within the BC1F2 segregating lines segregation was:
10 lines segregated 205R[188(;1):17(2)]:43S, P = .80-.90 for a 12:1:3 ratio
8 lines segregated 54R:146S , P = .30-.50 for a 1:3 ratio

The seedling reaction of Glenlea, Line W (W3563), F1, F2, F3 and BC1F2 to race C33(15B-1L) are presented in Table 23. The F1 seedlings were resistant [(;1) infection type] like Line W (W3563), indicating that the gene in Line W (W3563) is dominant and epistatic to the gene in Glenlea. The F2 population segregated: 108 seedlings had (;1) infection type, 11 seedlings had infection type (2) and 23 seedlings had infection type (4). This fitted satisfactorily the 12:1:3 ratio (P = .30-.50) indicating a two gene difference between the two cultivars; one dominant and one recessive. The F3 and BC1F2 lines that were resistant, susceptible or segregated to race C25(38), C65(38) and C49(15) were also resistant, susceptible or segregated to race C33(15B-1L) and their distribution conformed to the two gene hypothesis as indicated in Table 23.

TABLE 23. Stem Rust Reaction of F1, F2, F3 and BC1F2 of the Cross Glenlea/Line W (W3563) Inoculated with Race C33(15B-1L)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Glenlea	2	-	-			
Line W (W3563)	;1	-	-			
F1	;1	-	-			
F2	108(;1):11(2)		23	12:1:3	1.0234	.50-.70
F3	24	28	4	6:9:1	0.8889	.50-.70
BC1F2	23	18		1:1	0.6098	.30-.50

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:
15 lines segregated 353R[295(;1):18(2)]:62S, P = .25-.30 for a 12:1:3 ratio
7 lines segregated 130R:38S , P = .30-.50 for a 3:1 ratio
6 lines segregated 41R:107S , P = .30-.50 for a 1:3 ratio

Within the BC1F2 segregating lines segregation was:
10 lines segregated 207[188(;1):19(2)]:42S, P = .50-.70 for a 12:1:3 ratio
8 lines segregated 49R:135S , P = .50-.70 for a 1:3 ratio

Line W (W3563) X (WRT) ND71-13-1066

The seedling reaction of parental lines, F1, F2 and F3 to race C25(38) are presented in Table 24. The F1 seedlings were resistant [(0;) infection type] like (WRT) ND71-13-1066 indicating that the gene in (WRT) ND71-13-1066 is dominant and epistatic to that in Line W (W3563). The F2 population segregated: 95 seedlings had (0;) infection type, 25 seedlings had (;1) infection type, 6 seedlings had a (2) infection type and 1 seedling had a (4) infection type. This is a good fit to the expected 48:12:3:1 ratio (P = .75-.80) for three dominant genes difference between the two cultivars. Seventy F3 lines were also tested. Fifty-two lines were resistant [(0;), (;1) or (2) infection type], 18 lines segregated. No homozygous susceptible lines were observed. This fitted the 37R:26Seg:1S ratio (P = .01-.02) for three dominant genes. Within the resistant lines, 9 lines segregated for (0;) and (;1) infection types, 15 segregated for (0;), (;1), (2) infection types, 3 segregated for (0;) and (2) infection types and 1 line segregated for (;1) and (2) infection types. Within the segregating lines, 3 lines segregated for (0;), (;1), (4) infection types, 5 segregated for (0;), (2), (4) infection types, 4 segregated for (;1), (2), (4) infection types, 1 segregated for (0;), (4) infection types, 3 segregated for (;1), (4) infection types and 2 segregated for (2) and (4) infection types.

Under a three gene hypothesis, 40 F3 lines should be resistant [(0;), (;1) or (2)], 28 lines should be segregating and 1 line should be homozygous susceptible. Within the resistant lines 8 lines should segregate for (0;), (;1) infection types, 4 should

segregate for (0;), (;1), (2) infection types, groups of 2 lines should segregate for (0;) and (2), and (;1), (2), respectively. Within the segregating lines, 8 should segregate for (0;), (;1), (2), (4) infection types, groups of 4 lines should segregate for (0;), (;1), (4) and (0;), (2), (4), respectively, and groups of 2 lines should segregate for (0;), (4) and (;1), (4), infection types, respectively. The observed segregation had an excess of lines segregating for (0;), (;1), (2) infection types and a deficiency in lines segregating for (0;), (;1), (2), (4) infection types and the homozygous susceptible group. Eight lines within the 15 lines classified as segregating for (0;), (;1), (2) infection types must have been segregating for (0;), (;1), (2), (4) infection types. The failure to observe susceptible seedlings in these lines was possibly due to not having samples large enough to include susceptible seedlings. The segregation of F3 lines, therefore, was a satisfactory fit to the 37R:26Seg:1S ratio for three dominant genes. The three genes include Sr27 which conditions a (0;) infection, SrTt2 which confers a (;1) infection and the type (2) infection gene.

TABLE 24. Stem Rust Reaction of F1, F2 and F3 of the Cross Line W (W3563)/(WRT) ND71-13-1066 Inoculated with Race C25(38)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Line W (W3563)	;1	-	-			
(WRT) ND71-13-1066	0;	-	-			
F1	0;	-	-			
F2	95(0;):25(;1):6(2)		1	48:12:3:1	.5485	.90-.95
F3	52	18	0	37:26:1	8.2104	.01-.02

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:
3 lines segregated 68(0;):10(;1):2(4), P = .30-.50 for a 12:3:1 ratio
5 lines segregated 100(0;):20(2):5(4), P = .30-.50 for a 12:3:1 ratio
4 lines segregated 72(;1):22(2) :6(4), P = .70-.75 for a 12:3:1 ratio
1 line segregated 45(0;):10(4) , P = .20-.70 for a 3:1 ratio
3 lines segregated 60(;1):15(4) , P = .30-.50 for a 3:1 ratio
2 lines segregated 40(2):10(4) , P = .30-.50 for a 3:1 ratio

In tests with race C65(38) (Table 25), F1 seedlings were similar in reaction to (WRT) ND71-13-1066 [(0;) infection type], indicating that the gene in (WRT) ND71-13-1066 is dominant and epistatic to that in Line W (W3563). The F2 population segregated: 141 lines had flecks, 32 seedlings had (;1) infection type, 9 seedlings had type (2) infection and 1 seedling had type (4) infection. This was a good fit to the 48:12:3:1 ratio (P = .50-.70) for three dominant genes difference between the two cultivars. The F3 lines segregated as for race C25(38) conforming to the three gene ratio as indicated in Table 25.

TABLE 25. Stem Rust Reaction of F1, F2 and F3 of the Cross Line W (W3563)/(WRT) ND71-13-1066 Inoculated with Race C65(38)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Line W (W3563)	;1	-	-			
(WRT) ND71-13-1066	0;	-	-			
F1	0;	-	-			
F2	141(0;):32(;1):9(2)		1	48:12:3:1	1.4882	.50-.70
F3	52	18	0	37:26:1	8.2104	.01-.02

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregatinglines segregation was:

3 lines segregated	61(0;):11(;1):3(4),	P = .30-.50 for a	12:3:1 ratio
5 lines segregated	103(0;):21(2) :6(4),	P = .50-.50 for a	12:3:1 ratio
4 lines segregated	83(;1):18(2) :4(4),	P = .30-.50 for a	12:3:1 ratio
1 line segregated	37(0;):15(4) ,	P = .50-.70 for a	3:1 ratio
3 lines segregated	62(;1):18(4) ,	P = .50-.70 for a	3:1 ratio
2 lines segregated	48(2) :12(4) ,	P = .30-.50 for a	3:1 ratio

In tests with race C49(15) (Table 26), the F1 seedlings were resistant [(0;) infection type] like (WRT) ND71-13-1066 indicating that the gene in (WRT) ND71-13-1066 is dominant and epistatic to the gene in Line W (W3563). The F2 population segregated: 100 seedlings had flecks, 20 seedlings had (;1) infection, 4 seedlings had type (2) infection and 3 seedlings had type (4) infection. This fitted the 48:12:3:1 ratio (P = .50-.70) for three dominant genes. The F3 lines segregated as for races C25(38) and C65(38) indicating that the same three genes were effective against the three races as shown in Table 26.

TABLE 26. Stem Rust Reaction of F1, F2 and F3 of the Cross Line W (W3563)/(WRT) ND71-13-1066 Inoculated with Race C49(15)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Line W (W3563)	;1	-	-			
(WRT) ND71-13-1066	0;	-	-			
F1	0;					
F2	100(0;):20(;1):4(2)		3	48:12:3:1	2.0078	.50-.70
F3	52	18	0	37:26:1	8.2104	.01-.02

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:
3 lines segregated 80(0;):15(;1):4(4), P = .30-.50 for a 12:3:1 ratio
5 lines segregated 102(0;):19(2):3(4), P = .10-.20 for a 12:3:1 ratio
4 lines segregated 71(;1):24(2) :5(4), P = .30-.50 for a 12:3:1 ratio
1 line segregated 37(0;):8(4) , P = .25-.30 for a 3:1 ratio
3 lines segregated 62(;1):18(4) , P = .50-.70 for a 3:1 ratio
2 lines segregated 58(2):14(4) , P = .25-.30 for a 3:1 ratio

In tests with race C33(15B-1L) (Table 27), the F1 seedlings were resistant [(0;) infection type] like (WRT) ND71-13-1066, indicating that the gene in (WRT) ND71-13-1066 is dominant and epistatic to the gene in Line W (W3563). Sixty-nine F2 seedlings had (0;) infection type, 17 had (;1) infection type, 4 had type (2) infection. No susceptible seedlings were observed. This fitted satisfactorily the 48:12:3:1 ratio (P = .50-.70) for a three gene difference between the two cultivars. The F3 lines segregated as for races C25(38), C65(38) and C49(15) indicating that the three genes were effective against all

four races used.

TABLE 27. Stem Rust Reaction of F1, F2 and F3 of the Cross Line W (W3563)/(WRT) ND71-13-1066 Inoculated with Race C33(15B-1L)

Generation or parent	Infection type or breeding behaviour* R	Seg.	S	Expected ratio	Chi-square	P-value
Line W (W3563)	;1	-	-			
(WRT) ND71-13-1066	0;	-	-			
F2	69(0;):17(;1):4(2)	-	0	48:12:3:1	1.4935	.50-.70
F3	52	18	0	37:26:1	8.2104	.01-.02

*R = Resistant; Seg. = Segregating; S = Susceptible

Within the F3 segregating lines segregation was:

3 lines segregated 96(0;):19(;1):5(4), P = .30-.50 for a 12:3:1 ratio
5 lines segregated 97(0;):24(2) :4(4), P = .20-.25 for a 12:3:1 ratio
4 lines segregated 89(;1):27(2) :9(4), P = .50-.70 for a 12:3:1 ratio
1 line segregated 44(0;):11(4) , P = .30-.50 for a 3:1 ratio
3 lines segregated 51(;1): 9(4) , P = .25-.30 for a 3:1 ratio
2 lines segregated 62(2) :12(4) , P = .05-.10 for a 3:1 ratio

GENERAL DISCUSSION

Stem rust resistance genes SrTt2 and Sr27 and possibly another [type (2)] gene were transferred to Glenlea by successive testing and backcrossing to the recurrent variety Glenlea. Resistant seedlings carrying the SrTt2 gene or Sr27 gene were easily identified from segregating populations using the test race C25(38). These genes (SrTt2 and Sr27) confer a high degree of resistance and they normally displayed a (;1) and (0;) infection type, respectively; and are presently very effective over most Canadian stem rust races. The two Glenlea lines carrying the SrTt2 and Sr27 genes were designated Glenlea-T and Glenlea-R, respectively. Glenlea-T line carries the SrTt2 gene originally from *Triticum timopheevi* (McIntosh *et al.* 1971) while Glenlea-R line contains the Sr27 gene originally from Imperial rye (McIntosh 1973; Luig and Watson 1976).

The inheritance of seedling reaction to four wheat stem rust races was studied using F1, F2 populations and F3 and BC1F2 lines. Race C25(38) was used as a primary test race plus three other races: C65(38), C49(15) and C33(15B-1L). The results obtained relative to the inheritance of resistance of the cultivars Glenlea, (WRT) ND71-13-1066 and Line W (W3563), when crossed to the highly susceptible variety W3498, indicated that at least four genes were responsible for

resistance to the four stem rust races used. A single recessive gene was found to confer resistance against the four stem rust races C25(38), C65(38), C49(15) and C33(15B-1L) in Glenlea. Resistance due to a recessive gene, including the well known Sr17, has been reported a number of times (McIntosh *et al.* 1967; Watson *et al.* 1968; Oggema 1972). Glenlea has a parentage of fairly diverse origin and there is no direct evidence that Sr17 was responsible for its resistance. Glenlea, like Sr17, is effective against the four stem rust races used (Green 1976), and it is possible that Sr17 is responsible for resistance in Glenlea. However, the gene in Glenlea is effective against all Canadian stem rust races, while Sr17 is susceptible to some Canadian races (Green 1976). It is, therefore, possible that the recessive gene in Glenlea is a different gene and possibly a new gene yet unidentified.

Oggema (1972) reported a recessive gene in the Kenyan variety, Trophy, as well as another recessive gene in the variety Tobari 66 from Mexico. Tobari 66 has the parentage: Tezanos Pintos Precoz X Sonora 64, and therefore, has in common with Glenlea (Pembina^2 X Bage) X CB100 (where CB100 contains Sonora 64, Texanos Pintos Precoz and Nainari 60), the ancestors Sonora 64 and Tezanos Pintos Precoz. It is possible that Glenlea possesses the same recessive gene as Tobari 66 or there could be a different gene. Drs. E. Torres and S. Rajaram (personal communication) of CIMMYT, Mexico, citing from Martinez-Gonzalez (1972), pointed out that Sonora 64 has one dominant gene conferring resistance to race 12, the same or another dominant gene conferring resistance to race 113 and three dominant genes conferring resistance to races C25(38), C65(38), C49(15)

and C33(15B-1L). They also cited from Calderon-Perez (1975) that Tezanos Pintos Precoz has one dominant gene conferring resistance to isolate #570 of race 12 and two genes (one dominant and one recessive) conferred resistance to isolate #120 of race 12. The recessive gene reported to be present in Tezanos Pintos Precoz may be the same one detected in Glenlea or it could be another recessive gene.

(WRT) ND71-13-1066 has two dominant genes for resistance against races C25(38), C65(38), C49(15) and C33(15B-1L). The two genes include the Sr27 gene originally from Imperial rye (Acosta 1962; McIntosh 1973). Sr27 confers a very high type of resistance [(0;) infection type] to the four races. The other gene confers moderate resistance [type (2) infection] to all four races used. Sr27 is dominant and epistatic to the (2) type gene in the (WRT) stock ND71-13-1066. The nature and mode of inheritance of the moderate resistance gene in the background of a susceptible variety (W3498) was not studied. It may be possible that it could be one of the well identified Sr genes present in Thatcher, the recurrent parent of (WRT) ND71-13-1066 = (ND303*3//WRT238/5*Tc) or possibly a new gene from Imperial rye.

Line W (W3563) has one dominant resistance gene to races C25(38), C65(38), C49(15) and C33(15B-1L). Line W (W3563) contains the SrTt2 gene originally from *Triticum timopheevi* (McIntosh and Gyarfas 1971). It confers high resistance [(;1) infection type] to all the four races used, and it is resistant to most Canadian stem rust races.

Results from resistant X resistant inter-varietal crosses indicated a range of gene differences between cultivars. The Glenlea X (WRT) ND71-13-1066 cross indicated a three gene difference between the two cultivars when tested with races C25(38), C65(38), C49(15) and C33(15B-1L); two dominant and one recessive.

The Line W (W3563) X (WRT) ND71-13-1066 cross indicated a three gene difference between the two resistant cultivars when tested with races C25(38), C65(38), C49(15) and C33(15B-1L). No homozygous susceptible lines were observed in the F3 lines; this may have been due to too small a number to include susceptible lines. The three dominant genes include SrTt2, Sr27 and the type (2) gene, which the two cultivars contain, respectively. The Sr27 gene in (WRT) ND71-13-1066 is dominant and epistatic to the SrTt2 gene present in Line W (W3563).

The Glenlea X Line W (W3563) cross indicated a two gene difference between the two cultivars when tested to the four races; one dominant and one recessive. The two genes include SrTt2 and the recessive type (2) gene. SrTt2 was dominant and epistatic to the gene in Glenlea.

Gene expression to the four test races indicated that these genes were effective against all four wheat stem rust races and that each cultivar had one or two resistance genes. The results indicated that when two or more resistance genes were incorporated into a cultivar, the infection type was usually typical of the resistance gene conferring the highest level of resistance. This is in accordance to Hooker (1967) that genes that condition a higher level of resistance

are commonly epistatic to those conditioning a less resistant reaction.

The added resistance genes (SrTt2 and Sr27) in Glenlea makes this cultivar much more resistant to current Canadian stem rust races. However, their usefulness should be investigated further in terms of their effect on the yielding ability of Glenlea.

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