The inheritance of resistance of barley (Hordeum vulgare L.) to Rhynchosporium secalis (Oud.) J.J. Davis
by Moncef Mohamed Harrabi

A thesis submitted in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Plant Pathology
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Abstract:
Research was initiated to gain a better understanding of the inheritance of reaction to Rhynchosporium secalis (Oud.) Davis in some barley cultivars and lines that are components of the recurrent selection population (Rrs-5). F2 plants resulting from different crosses were screened for seedling resistance to three isolates of R. secalis. Further evaluation of some F2 populations was done under disease conditions in the field to one isolate from Montana. Some of the culti-vars that were studied for inheritance of resistance were further evaluated in terms of their combining ability for yield and yield components.

Further studies were done to estimate the change in gene frequencies for resistance to scald after four cycles of recurrent selection. The total number of genes conditioning scald resistance is probably not as large as previously believed. Evidence was presented on the existence of a series of multiple alleles at the Rh-Rh3-Rh4 locus complex. Further evidence on the existence of resistance factors in susceptible cultivars was shown by crosses between susceptible cultivars. Transgressive segregation indicated the presence in barley of minor genes for scald resistance.

No significant build up in resistance between different cycles of recurrent selection was observed. This was attrib-uted to either the inability to combine multiple alleles in any single pure line or to insufficient natural disease infections at different nurseries. The probability, however, of selecting plants resistant to isolates representing a wide range of virulence types from the recurrent selection popula-tions is high.

In dedication to:

my wife Hajer, my daughters Ons and
Maysem, my son Aymen, my father and mother.

THE INHERITANCE OF RESISTANCE OF BARLEY (*HORDEUM VULGARE* L.) TO *RHYNCHOSPORIUM SECALIS* (OUD.) J. J. DAVIS

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ABSTRACT

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Chapter 1

INTRODUCTION

Scald of barley (Hordeum vulgare, L.) caused by Rhynchosporium secalis (Oud.) Davis is a destructive disease of barley that can seriously limit yield in many humid and sub-humid growing areas. The disease is considered of minor importance in the northcentral North American spring barley area, but causes considerable damage along the Pacific coast, Europe, Asi, the Middle-East and Australia.

Changes in agricultural practices (minimum tillage, continuous cropping, etc.) have influenced the microclimate and resulted in more residues favorable for the scald organism. Control of this disease has been achieved mainly by genetic resistance. At least fifteen alleles for scald resistance have been described, but their genetics are only partially clarified. Starling et al. (1970) believed that scald resistance genes were not numerous. They assumed that most of the resistance genes are located at the Rh-Rh3-Rh4 locus complex on chromosome 3. It is not known if these genes are alleles or closely linked. Dyck and Schaller (1961) reported that the Rh-Rh3-Rh4 genes were linked and not allelic. None of the recessive genes rh6, rh7 and rh8 have been tested for allelism against Rh-Rh3-Rh4, Rh3 or Rh5. Rh9 has not been tested for allelism with any other locus.

If the number of genes for scald resistance is much smaller, then

developing pure line cultivars with long term resistance may be extremely difficult, if not impossible. As new genes for resistance have been incorporated into suitable agronomic cultivars, the pathogen has mutated resulting in breakdown of resistance, and thus a short term control (Jackson and Webster, 1976).

Recently resistance factors that are not specific in their action have been demonstrated in different host-pathogen interactions. The theoretical value of this type of resistance is that it operates indiscriminately to all pathogen races and provides a durable resistance. If genes controlling different components of this type of resistance can be identified then recurrent selection techniques represent a valuable tool in building quantitative resistance. The objectives of this study were to: (1) gain more understanding of the genetics of resistance of some barley cultivars, (2) measure changes in resistance in different cycles of recurrent selection to different isolates of Rhynchosporium secalis, and (3) determine the potential of some component cultivars of the recurrent selection population in terms of their combining ability to disease reaction, yield and yield components.

Chapter 2

LITERATURE REVIEW

The Pathogen: *Rhynchosporium secalis*

Barley leaf scald caused by the pathogen *Rhynchosporium secalis* was first described by Oudemans in Holland in 1897 who named it *Marsonia secalis* (Oudem). In 1900, Heinsen, in Germany, put the fungus in a new genus *Rhynchosporium* because of the beaked one-septate spores, and named it *Rhynchosporium graminicola Heinsen*. Formal descriptions were later provided by Saccardo who credited authority for the genus *Rhynchosporium* and *R. graminicola* to Heinsen. In 1922, Davis, in the United States, named it *Rhynchosporium secalis* (Oudem) J. J. Davis and it is by this name that the fungus is presently known. Caldwell (1937) described the fungus in the following manner:

> Parasitic, producing spots on leaves; sterile mycelium sparse in mesophyll of host; mycelium subcuticular at first, later developing into a superficial fertile stroma more or less covering the leaf spot; conidiophores absent; conidia one-septate, hyaline, sessile on cells of fertile stroma.

The genus, *Rhynchosporium*, would fall in the classification, Moniliaceae Hyalodidymae, Micronemeae of the imperfect fungi. The conidia of several isolates from the host and from culture show a relatively homogeneous shape and size. The conidia length and diameter are 15.8 ± .21 and 3.3 ± .05 micrometers respectively (Caldwell, 1937). One-celled conidia in which the septum had not formed had only one nucleus, while two-celled spores had a nucleus in each cell (Caldwell, 1937).

Since R. secalis is uninucleate, heterokaryotic phenomena problably do not apply. Variations in the fungus must occur through mutations, parasexual cycle or even environmentally-induced changes. A population of R. secalis, made up by mixing four races in equal frequencies, has resulted in 18 races after only two successive disease cycle on a susceptible host (Jackson and Webster, 1976). This clearly demonstrates that the natural gene pool of R. secalis is probably very large. Caldwell (1937) had no success in obtaining the perfect stage of the fungus. Skoropad and Grinchenko (1957) discovered microconidia suggesting the possible existence of a sexual cycle. A few years later Ali (1972) also observed microconidia being exuded from flask-like mycelial branches but these microconidia failed to germinate and probably were spermatia.

The major source of primary inoculum appears to be from infected plant debris (Caldwell, 1937; Skoropad, 1960; Ayesu-Offei and Carter, 1971). Heinsen (1901) noted the saprophytic capability of the fungus in the greenhouse where its viability was maintained for a period of 15 months. This finding was also supported by Bartel (1929) who reported a six month survival of the fungus in infested soils. Survival of the fungus under saprophytic conditions in the soil has not been substantiated by later authors (Caldwell, 1937; Skoropad, 1962). The information on seed-borne inoculum is contradictory. Caldwell (1937) used barley seed from severely infected plants in soils with no

previous scald history. No scald infections appeared in his trials. This perhaps does not indicate clearly that the fungus is not seed-borne since infected plant fragments may accompany the seed. However, Reed (1957) has shown that the fungus can be seed-borne. The ease of the spread of the disease to new barley areas suggests that there is some means of long-range dissemination of R. secalis. There is no evidence that volunteer barley can serve as a source of inoculum (Reed, 1957; Ali, 1974; Caldwell, 1937). Like most leaf-infecting organisms, R. secalis overwinters as dormant mycelium on barley residues (Skoropad, 1959).

Symptoms. Rhynchoporium secalis affects any parts of the leaves including the leaf sheath producing spots of irregular shape (Brooks, 1928; Reed, 1957; Ali, 1974; Caldwell, 1937). In addition, the barley auricles are commonly attacked, perhaps because of the tendency for water to collect in this region (Brooks, 1928). Infection in early stages occurs as bluish-gray lesions with a water-soaked appearance. As invasion advances, the center of the lesions usually dry out and become light gray to grayish white with a dark brown edge. Lesions may develop separately and then coalesce or may develop progressively along the leaf. Symptoms under greenhouse conditions vary somewhat. Usually there is no definite lesions except color change of the leaf which becomes light gray to gray-green. This phenomena is observed in most cases. Tissue collapse takes place quickly and drying occurs

shortly after. Smith (1938) and Skoropad (1957) observed conspicuous scald lesions on the chaff of the grain. The authors both suggested that seed may serve as a source of primary inoculum. Shipton et al. (1974) reported that floral bracts awns and pericarp are readily infected. This is perhaps a further evidence of possible seed transmission of the fungus. Hypersensitive reaction which resulted in the formation of small dark-brown patches on the leaves has been reported by Ayesu-Offei and Clare (1971).

Pathological histology. The pathogen-host tissue relationship has been studied by few workers. Condia of R. secalis germinate from one or both cells in 12 hours at 13 C forming short germ tubes and appressoria (Shipton et al., 1974; Ayesu-Offei and Clare, 1970; Caldwell, 1937). The first germ tube usually arises from the large cell and the second came from the other cell. In some cases two germ tubes developed from a single cell. The germ tubes are septate, usually about 0.8 micrometers in diameter and 20.30 micrometers in length (Ayesu-Offei and Clare, 1970). After their formation some germ tubes enlarge to form appressorium and penetrate the cuticle within a period of 24 hours after inoculation (Ayesu-Offei and Clare, 1970). The authors further stated that appressoria was not essential for penetration and the penetration does not occur through stomata as reported by Bartels (1928) but occurs directly as has been reported by Caldwell (1937). Enzymatic degradation of the cuticle may provide the

initial penetration. Following penetration, the infection hyphae grows rapidly between the cuticle and the epidermis. This is followed by a subcuticular mycelium growing between epidermal cells and branching profusely (Shipton et al., 1974). The subcuticular hyphae imparts a grayish cast to the infected area. Mesophyll cells beneath subcuticular hyphae soon collapse, possibly due to toxic substance(s) produced by the hyphae. Cell disruption may be caused by a toxin, Rhynchosporoside, one of the 1-O-α cellobiosides of 1,2. Propanediol (Beltran et al., 1980). The fungus may be responsible for the increase in the permeability of host cells so that the concentration of nutrients in the free space is increased for use by the fungus (Jones and Ayres, 1972). The authors reported no evidence of toxic metabolites produced by R. secalis as opposed to the finding of Ayesu-Offei and Clare (1970) and Beltran et al., (1980). No entry of the fungus through stomata have been reported except by Bartels (1928). Ayres (1972) has observed increased stomata opening in areas of the leaf colonized by the fungus.

Factors affecting infection and symptom expression. Host-pathogen and environmental interactions are responsible for infection and colonization of the host by the pathogen. Phenotypic variability in disease expression is associated with host genotype, pathogen-genotype and environmental factors at the time of interactions (Shipton et al., 1974). Relative humidity as well as temperature appear to be the limiting factors in successful infection (Shipton et al., 1974;

Caldwell, 1937; Brooks, 1928; Skoropad, 1962a and 1959; Fowler and Owen, 1971). Temperatures around 20 C are the most favorable for conidia production and germination (Caldwell, 1937; Shipton et al., 1974; Skoropad, 1957 and 1962; Reed, 1957). Ayrea and Owen (1970) reported failure of conidial germination in lesions due to the presence of self-inhibitors. At high concentration (120,000 spores/ cm^3) spore germination does not cease. The inhibitor apparently feeds back at high concentrations to inhibit its own production (Ayres and Owen, 1970). Fowler and Owen (1971) reported that on intact plants spore germination increased slightly with increasing concentration of spores. Optimal germtube elongation occurs at a temperature range of 18 - 21 C. Temperatures above 30 C resulted in conidial rupture (Caldwell, 1937). Reed (1957) observed the shortest germtube growth at 7 C, and that the maximum growth rate of the R. secalis isolates occurred at a pH of 5.2 which is close to the pH of 5.6 expressed in barley leaf juices.

Skoropad (1957) observed that lesions appeared most rapidly when inoculated plants were held in saturated air at 15 - 18 C for 48 hours and then moved to a greenhouse held at about 24 C. Using both susceptible and resistant cultivars, Ali (1972) noted that at high diurnal temperature regimes (18 C min/30 C max) certain isolates lose the ability to infect hosts normally susceptible to them. Low

temperature (8 - 20 C) favored certain isolates while others are enhanced at higher temperatures (15 - 24 C). Lesion development proceeds normally at post-inoculation temperatures around 20 C and is slowed down or ceases at low temperature (6 - 12 C) and at high temperature (24 C) (Shipton et al., 1974).

Few experiments have been conducted on the influence of host stage of development on symptom expression. Ali (1972) reported that genotype age may influence symptoms. Greater symptom expression occurs at anthesis probably due to tissue senescence.

Physiological races. Many authors have shown the existence of races of Rhynchosporium secalis (Shipton et al., 1974; Schein, 1958 and 1960; Reed, 1957; Caldwell, 1937; Williams and Owens, 1973; Owen, 1958 and 1963). No specialization of isolates into races from barley was recognized until 1955, although Sarasola and Campi (1947) in Argentina have differentiated four races. Riddle and Suneson (1948), in field trials at Davis, California observed no evidence of physiological races. Later Schein (1958) found five races based on their ability to attack the barley cultivars Wisconsin winter x Glabron, Brier, Hudson, California 1311, Atlas 46 and Turk. Schein (1960), working with eight isolates from different parts of the U.S., differentiated seven races which he designated U.S. 1 to U.S. 7. Later, Dyck and Schaller (1961a) identified two additional races, U.S. 8 and

U.S. 9. Kajiwara and Iwata (1963) reported the existence of ten races in Japan. Reed (1957) showed the presence of races of R. secalis in Canada and the U.S., however Skoropad (1960) found no clear evidence of pathogenic races in Canada. Williams and Owen (1973) tested 122 single spore isolates of R. secalis collected from Britain on 12 cultivars of barley and were able to find two distinct races which they called U.K. 1 and U.K. 2. Earlier Owen (1963) working with ten British isolates demonstrated variability within R. secalis but could not distinguish any races present at that time. Recently Ceoloni (1980) in Italy, using 13 barley cultivars with known genes for specific resistance to scald, was able to differentiate 17 races. Atlas and Atlas 46 were resistant to all Italian isolates. This clearly demonstrates the difference between the U.S. and the Italian races. In California, both Atlas and Atlas 46 are very susceptible (Jackson and Webster, 1975). Further, the Italian races appear to be different from those reported by Owen (1963) in Britain. La Mesita, resistant to Owen's isolates, was susceptible to ten of the Italian races.

Ali (1972) found 15 biotypes from a collection of 35 isolates from Western Australia. The author studied the performance of these 15 biotypes under summer and winter conditions and was able to detect marked differences in host response, suggesting that environmental conditions at the time of testing may influence the interpretations.

Kajiwara and Iwata (1963) found that substrate composition and culture age can influence virulence. Hansen and Magnus (1973), working with 11 barley cultivars, found 11 different virulence genes in Norway. The virulence genes r8, r9 and r10 were most predominant in Norway.

Epidemiology. Several investigators have reported on the persistence of R. secalis as mycelium in barley debris (Skoropad, 1960; Caldwell, 1937; Reed, 1957; Shipton et al., 1974; Ayesu-Offei and Carter, 1971). Skoropad (1966) reported that scald lesions retained their ability to produce conidia for up to 340 days, depending on environmental conditions. In earlier studies, Skoropad (1960) suggested that after development of the first lesion, secondary inoculum was dispersed by wind-born rain splash. He further found that conidia are most abundant during rainstorms and that they are clustered in groups of three to ten, indicating transport of conidia in water droplets. Ayesu-Offei and Carter (1970) found that sporulation occurred most abundantly when free moisture is present. They further observed that fewer conidia were trapped under dry but windy conditions. Wind tunnel experiments indicated that conidia were trapped under dry, windy conditions. These experiments indicated that conidia are released and dispersed mainly as a result of water splash and not due to wind alone (Ayesu-Offei and Carter, 1970). In addition, they found that conidia are released at any time of the day or night, which is in contradiction to the finding of Ozoe (1956) who claimed that the

number of conidia of R. secalis in the air is greater in the day time.

Disease spreads from plant to plant and pockets of infection may appear as far as nine meters from the nearest source of inoculum (Reed, 1957; Ayesu-Offei and Carter, 1970). No evidence was found indicating spread of R. secalis by insects.

Economic importance. Scald, incited by Rhynchosporium secalis is a common foliage disease of barley in many parts of the world. Frank (1897) first reported the disease in Germany and recognized it to be of a major economic importance, especially when the plants were attacked before heading. The disease was first mentioned in the United States in 1917 (Caldwell, 1937). Today scald is known to occur in Northern Europe, United States, Canada, England, Middle East, North Africa, Mexico, Argentina and Peru. The first epidemic in the United States was reported in the interior valleys of California (Caldwell, 1937). Not only have seasonal conditions favored the disease development and outbreaks, but also the changes in agricultural practices (minimum tillage, sprinkler irrigation, close rotations, combine harvesters, etc...) have contributed significantly (Shipton et al., 1974).

Wiebe, as reported by Caldwell (1937) estimated yield losses up to 15 percent based on comparative yields of susceptible and resistant varieties during epidemic and non-epidemic years. In Wisconsin, scald completely destroyed spring barley plots when infection occurred early

in the season (Caldwell, 1937). In England, yield losses between 35 and 40 percent have been reported (Shipton et al., 1974). James et al. (1968) have found that yield reduction occurs mainly through reduction in kernel weight. If infection occurs early in the season, number of tillers per plant may also be reduced.

In an extensive study between yield loss and disease caused by R. secalis, Clives et al. (1968) compared yields from plants sprayed with fungicide with those from unsprayed plots. They further compared yields of cultivars with varying susceptibility level to the disease. Yield loss was found to be equivalent to two-thirds of the percentage of the flag-leaf area visibly infected or one-half of the infected area on the second leaf. Clives et al. (1968) used the average of these two estimates to predict yield loss.

Inheritance of Resistance

Losses caused by R. secalis stress the need for the development of cultivars resistant to the scald organism. In order to facilitate this objective in a breeding program, a thorough understanding of the manner of inheritance of reactions to the disease becomes a necessity.

The most extensive and earlier work on the genetics of scald resistance was reported by Dyck and Schaller (1961). They reported five genes for resistance and designated them as Rh2, Rh3, Rh4, $Rh4^2$ (an allela of Rh4) and Rh5. These workers found a single dominant gene (Rh2) in Atlas. Atlas 46 has a second gene (Rh3) in addition to

the Rh2. Atlas 46 is a derivative of a cross between Atlas and Turk. Turk was found to have two dominant genes (Rh3 and Rh5) by Riddle and Suneson (1950) and Dyck and Schaller (1961a). Other workers reported Turk as having only one gene (Evans, 1969; Baker and Larter, 1963; Wells and Skoropad, 1963; Starling et al., 1971; Ali, 1975a). Ali (1975b) found that the gene in Turk is allelic or closely linked to that of La Mesita.

La Mesita has been reported to possess one dominant gene Rh4 (Riddle and Briggs, 1950; Dyck and Schaller, 1961; Starling et al., 1971). Habgood and Hayes (1971) found that La Mesita contains two genes (Rh4 and Rh10). Ali (1975b) also reported on the existence of two genes in La Mesita, one of them probably being the same as Rh4 found is Osiris reported by Dyck and Schaller (1961). Baker and Larter (1963), in evaluating F_2 and backcross families, found that Jet and Steudelli each had two temperature sensitive complementary recessive genes designated rh6 and rh7. Temperatures greater than 25 C induced a susceptible reaction in Jet and Steudelli. Thus, that the usefulness of these two varieties in a breeding program is limited due to the temperature sensitivity of their resistant genes. Resistance of both Abyssinian (CI668) and Kitchin is controlled by a single gene that shows incomplete dominance and designated Rh9. This gene confers full resistance only in a homozygous condition. In an early study Riddle and Briggs (1950) have found that both Trebi and Modoc had a

dominant and a recessive gene for resistance to scald. This is possible since Trebi was one parent of a composite cross from which Modoc was derived. The dominant gene is identical to the one in La Mesita (Riddle and Briggs, 1950). These authors also reported that Turk has two dominant genes, one of which is similar to the one present in La Mesita, Modoc and Trebi. Other workers have reported the existence of only one gene in Turk (Baker and Larter, 1963; Evans, 1969; Wells and Skoropad, 1963). Habgood and Hayes (1971), on the other hand, found one dominant and one recessive gene in Turk.

Dyck and Schaller (1961a) observed that Osiris contains only one gene which is dominant and probably the same as the one found in La Mesita (Rh4). Wells and Skoropad (1963), however, reported that Osiris contains one gene Rh3 similar to the one found in Atlas 46. Furthermore, Ceoloni (1980), working with Italian isolates of R. secalis, reported that the genes of La Mesita and Osiris are different. Habgood and Hayes (1971) suggested the presence of an additional recessive gene (rh6) in Osiris when compared to La Mesita. These workers reported that this gene acts as a "neutral" one in cultivars other than Jet in which it was originally found. Thus Osiris may contain two dominant genes (Rh 4 and Rh10) and one recessive gene (rh6) (Hapgood and Hayes, 1971).

Hansen and Magnus (1973), working with Norwegian isolates, clearly showed that the resistance in La Mesita and Modoc was not conditioned

by identical genes. This appears to contradict the findings of Hapgood and Hayes (1971) who consider the genes for resistance in Turk, Atlas 46, Modoc, Osiris and La Mesita to be at the same locus. In an earlier study Riddle and Briggs (1950) found that the varieties La Mesita, Trebi and Modoc had a single dominant gene in common for scald resistance.

The gene rh8 in Nigrinudum has been reported by Wells and Skoropad (1963) and confirmed by Habgood and Hayes (1971). These last workers have also shown that the complementary recessive gene (rh7) in Jet is situated at the Rh locus. They amended the designation of rh7 reported by Baker and Larter (1963) to rh5. The rh6 was retained for the other gene which is present in Turk, Modoc and Osiria. A fourth recessive gene, rh11, was reported by Habgood and Hayes (1971) in CI4364 and CI4368. The results of these workers show that there are five alleles at the Rh locus; two are dominant Rh and Rh^2), two have complete dominance (Rh3 and Rh4) and one is recessive (rh5). Multiple alleles have also been shown at the Mla locus conditioning mildew resistance in barley (Moseman, 1966).

Dyck and Schaller (1961) have assigned Rh3 and Rh4 to linkage group 3. These authors have found that the Rh3 gene was linked to a gene-conditioning spike density with a recombination value of 14 ± 1.56 percent, and was closely linked with a gene for streaked seedlings; and that Rh4 was linked with a xantha seedling gene with an estimated

11.2 ± 1.21 percent recombination value.

The genetics of resistance of the cultivars mentioned above is not clear and more complicated than suggested by previous literature. Differences could be due to multiple alleles or to genes closely linked. The detection of certain genes that confer resistance and their identification with other previously described genes depends on the virulence of the genes in the genetic studies and also on the prevailing environmental conditions. It has clearly shown that the resistance of Jet and Steudelli is temperature sensitive and breaks down at temperatures above 25 C (Baker and Larter, 1963).

Fowler and Owen (1971) studied the mechanisms of resistance to R. secalis. They reported that the earliest point at which resistance was expressed was at penetration of the cuticle. Cutin thickness does not contribute to this resistance. Cutin acids, have been reported to be more prevalent in leaves of resistant strawberry to Sphaerotheca macularis (Fr.) Jaczev. than in leaves of susceptivle cultivars (Peries, 1962). Conidia of Erysiphe graminis germinated, and appressoria were formed at the same rate on all tested barley cultivars whether resistant or susceptible (White and Baker, 1964). Ayres and Owen (1971) found that host resistance did not affect germination or appressorium formation of R. secalis.

Recurrent Selection Populations

The prevalence of the disease and the extent of the damage it can

cause have necessitated the development of resistant cultivars. There are two major types of resistance that are of importance in breeding programs, race specific and race non-specific resistance.

Race-specific resistance has been extensively utilized in the past to produce extremely resistant cultivars (Evans and Griffiths, 1971). This approach presents serious disadvantages and often has resulted in "boom and bust" cycles. Atlas 46, a race specific resistant cultivar to California races of R. secalis, was released in 1947. Nine years later resistance broke down and Atlas 46 became susceptible. Today there is growing interest in resistance which is not race-specific. The winter wheat cultivar Crest, for example, has three minor genes conditioning resistance to stripe rust and has been cultivated for the past 15 years without loss of resistance (Sharp et al., 1976). Moro, on the other hand, with only one major gene for resistance to stripe rust lost its resistance a few years after its release.

The use of single major genes for resistance to any disease remains an attractive method for plant breeders because of ease of incorporation and selection. Breeding for race non-specific resistance however, is more difficult to achieve, specially if this type of resistance shows both continuous variation and a genotype-environment interaction (Evans and Griffiths, 1971).

Recurrent selection is an effective breeding method of accumulating genes and developing multigenic resistance (Barnes et al., 1971). It

was first proposed by Hayes and Gerber (1919) and has been used extensively to improve breeding populations of maize (Moll and Stuber, 1971).

Many recurrent selection methods have been proposed to improve breeding populations (Sprague and Eberhard, 1977). They require the selection of plants with superior genotypes from the population and the intermating of these selected individuals to form a new population. Thus recurrent selection gradually increases the frequency of favorable alleles. This increase depends on the ease by which superior individuals are identified and on the number of genes controlling a specific trait. Barnes et al., (1971) subjected two unrelated populations of alfalfa to bacterial wilt (Corynebacterium insidiosum (McCall) Jens). They were able to reduce the disease severity indices rather rapidly in one population which apparently possessed major genes. The disease severity reduction, however, was slower in the second population which probably contained minor genes.

The average rating for leaf feeding by the European corn borer (Ostricia nubilalis Hubner) was reduced from 5.4 to 2.9 (1 to 9 scale) in only three cycles of recurrent selection (Penny et al., 1967). An average reduction of 2.8 percent of ears with kernel damage due to the feeding of earworms (Heliothis zeae Boddie) per cycle of recurrent selection was reported by Zuber et al. (1971). Jenkins et al. (1954) used phenotypic recurrent selection to reduce

the disease rating to leaf blight (Helminthosporium turcicum Pass.) from 3.3 to 2.1 (on a 0 to 5 scale) after three cycles. Stalk-rot resistance (Diplodia zeae (Schw.) Lev.) was also improved by recurrent selection (Jinahyon and Russell, 1969).

Phenotype recurrent selection was also used to improve quantitative traits. Russell and Eberhart (1970) reported that additive genetic variation for yield and other quantitative traits is sufficient to obtain progress from recurrent selection. A yield increase in corn of 5.2 q/ha has been reported by Eberhart et al. (1973a). In order to achieve a positive genetic gain, plants with superior phenotypes must be selected in the breeding population. Inbreeding may be a serious problem in these populations but can be avoided when a sufficient number of plants is selected after each cycle. Thus population size needs to be taken into consideration.

The method has its greatest success in breeding cross-pollinated crops. Its usefulness in self-pollinated species is limited because of the difficulty in obtaining large number of crosses for recombinations. This difficulty is circumvented in barley by utilizing genetic male sterility to facilitate crossing. A number of male sterile genes have been identified in barley (Hockett et al., 1968) since the first one described by Suneson (1940). Suneson (1956) utilized genetic male sterility in several composite crosses. He relied on natural selection to improve population characteristics.

Chapter 3

MATERIALS AND METHODS

Inheritance of resistance

Materials. The barley tested for scald resistance consisted of (a) a number of cultivars and strains of spring barley from different areas of the world with known genes for scald resistance to strains from the United States and Europe, (b) selected cultivars with good agronomic characters and wide adaptation, (c) lines with unknown genes for resistance to scald, (d) F_1 and F_2 lines from all possible crosses of some selected lines. The parents and their Cl numbers are listed in Appendix Table 1.

Inoculum preparation. The fungus was cultured on lima bean agar in an incubation chamber at 18 C and eight hours of light. The Montana isolate used in these studies originated from scalded plants collected from Lewistown, MT. in 1975. The Tunisian (Tun.1), California (Ca.75) and Morocco (Mor.25) isolates came from lyophilized cultures maintained in the refrigerator. Subsequent culturing was done by transferring spores to fresh lima bean agar plates with autoclaved Q-tips. Cultures to be used as inocula were started on the same day that the barley plants to be inoculated were planted and harvested two weeks later. The method of Schein and Kerelo (1957) for isolation of the disease organism was used.

The inoculum was prepared by flooding two week old plates with

distilled water and scraping the colonies with a microscope slide. The resulting spore suspension was filtered through four layers of cheese cloth to remove mycelial and agar fragments. A Levy-Hausser counting chamber No. 508 (Hausser Scientific) was used to measure spore concentration. The inoculum was standardized at 6 x 10^6 spores/ml and applied with a DeVilbiss atomizer attached to a compressed air hose (15-20 psi). Each flat in the greenhouse was sprayed with 25 ml of spore suspension and transferred to a dark dew-simulation chamber kept at 20 C for 24 hours, then returned to the greenhouse. Two weeks later scald readings were recorded using a 0 to 3 scale. (0 = no visible lesion, 1 - marginal lesions, 2 = small lesions not confined to leaf margins and 3 = typical scald.)

F_2 progeny field studies. Two hundred F_2 seeds from each cross and their parents were space planted at the Horticulture Farm at Bozeman, MT. in May 1981. The individual plants were spaced 6 cm apart in rows 6 m in length and 35 cm apart.

Inoculation was made in later afternoon with a Montana isolate (Lew B77) a few weeks after seeding. All entries were sprinkler irrigated before and after inoculation for five minutes to maintain a humid environment. Inoculation was repeated two weeks later to assure infection. Each row was sprayed with a spore suspension using a solo mist sprayer (Solokleinmotoren GMBH, West Germany). A generally good infection was obtained. Scald symptoms began to appear on the plants

in the middle of June. Scald readings were made in July and early August using a disease intensity rating scale of 0 to 3 of resistant (0), intermediate (1, 2) and susceptible (3).

F_2 progeny greenhouse studies. Each F_2 population was grown in a metal flat (14" x 10" x 3") containing about 200 seeds. Both parents of each cross were also seeded in the beginning of each flat. All flats were kept in the greenhouse maintained at about 20 C. During warm days temperature had risen to about 27 C. Two weeks after sowing each flat was sprayed with 25 ml of spore suspension adjusted to about 6×10^6 sproes/ml and applied with a DeVilbiss atomizer attached to a compressed air hose (15-20 psi). Flats were transferred to a dew-simulation chamber with an air temperature of about 20 C for 24 hours. The flats were then returned to the greenhouse. Two weeks later scald readings were made.

Statistical procedures. In most instances 0, 1 and 2 reactions were grouped together as resistant and a 3 reaction was classified as susceptible. In other 0, 1 and 2 and 3 reactions were classified as resistant, intermediate and susceptible, respectively. Chi-square was used to determine if the observed classes fit a hypothetical genetic ratio.

Recurrent selection population studies

A male sterile-facilitated recurrent selection population, designated Composite Cross XXXVI, was developed to select for

broad-based resistance to scald, incited by Rhynchosporium secalis (Oud.) J. J. Davis. A description of this population, including parents, assembly, and the recurrent selection cycle appears elsewhere (Bockelman et al., 1980).

Five stages (representing four cycles of recurrent selection) in the development of C.C. XXXVI were chosen for use in this study, as follows:

Stage 1: Initial population after assembly.

Stage 2: Stage 1 after planting in a disease nursery at Bozeman (1976), inoculation with a Montana isolate of R. secalis (Lew B77), roguing of the susceptible plants (40%), and harvesting seed on the remaining male sterile plants.

Stage 3: Stage 2 after recombination nursery in Arizona, planting in a disease nursery at Bozeman (1977), inoculation (Lew B77), roguing of the susceptible plants (25%), and harvesting seed on the remaining fertile plants.

Stage 4: Stage 3 after recombination nursery in Arizona, planting in disease nurseries (1978) at Bozeman (inoculated Lew B77, rogued 10%), Fairfield, MT

(natural infection, rogued 5%), and Ft. Benton, Mt (natural infection, rogued 5%), harvesting seed on fertile plants and bulking (44, 44, 12% respectively) along with seed (15% of total bulk) harvested from disease nurseries (planted to seed of stage 2) in Georgia (natural infection, fewer than 100 resistant plants harvested), Maryland (natural infections, 20 resistant plants harvested, and Izmir, Turkey (natural infection, fewer than 100 resistant plants harvested.

Stage 5: Stage 4 after 1) recombination nursery in Arizona; 2) addition of seed harvested from disease nurseries (planted to seed of stage 3) at Woodland, CA (natural infection, 150 resistant plants harvested) and Beja, Tunisia (light infection, 200 agronomically better plants selected) (16, 9% added respectively); and 3) planting in disease nurseries (1979) at Bozeman (inoculated Lew B77, rogued 30%), Fairfield (natural infection, rogued 5%), Ft. Benton (natural infection, rogued 5%), Davis, CA (natural infection, rogued 70%), Suweon, Korea (natural infection, 200 resistant plants and bulked (49, 4, 4, 25, 12, 6% respectively).

Seeds from the five stages were planted in a disease nursery at Bozeman, MT in 1980, using a randomized complete block design with four replications. Each plot in a replication contained about 50 plants from a stage which were grown in two, three meter rows. A 30 cm spacing was used between the rows. A spore suspension was streaked on lima bean agar and incubated for two weeks at 18 C. The agar with the fungus were comminuted with a blender. Inoculation was performed with the resulting spore suspension (about 6×10^6 spores/ml) using a Solo mist sprayer (SoloKelinmotoren GMBH, West Germany) four weeks after sowing with only one isolated from Montana (Lew B77).

Plants from the five stages were also grown in the greenhouse in metal flats. Four flats, each containing one replication of each cycle with approximately 100 seeds, were used. The greenhouse inoculations were done with three isolates representing a diversity in virulence. The isolates were from Montana (Lew B77), California (Ca. 75) and Tunisia (Tun.1) and were incubated as described above. The inoculum was adjusted to about 6×10^6 spores/ml. Each flat was sprayed with 25 ml of the spore suspension using a tip atomizer attached to an air hose. Flats were then placed in a dew-simulation chamber for 24 hours at 20 C. These flats were then returned to the greenhouse, maintained at about 20 C for two weeks, then readings were made. A disease rating scale of 0 to 3 was used: 0 = no visible lesions, 1 - marginal lesions only, 2 - small lesions not confined to leaf margins, and 3 = typical

scald lesions with total collapse of the leaf. Plants with 0, 1 and 2 infection types were pooled and classified as resistant. Fifty plants in the field were tagged so that measurements of yield and yield components could be made at harvest time. The frequencies of resistant plants in each cycle were calculated along with analysis of variance and correlation matrices.

In another study, about 200 plants were chosen at random from stages 1, 3 and 5. Each plant was harvested separately and equal amounts of seed from each plant was bulked. The resulting mixture was seeded in Arizona. Two hundred spikes from each cycle were chosen at random and harvested separately. Equal amounts of seed from the 200 spikes was bulked and seeded at the Horticulure Farm, Bozeman, MT, in April of 1981. In September 1981 again 200 spikes from each of the three stages were chosen at random and harvested separately. Equal amounts of seed from each spike was bulked. Up to the third generation no selection for scald resistance has been practiced and at least 75 percent homozygosity has been achieved. About 200 seeds from each stage were grown in metal flats and were inoculated with three scale isolates Morocco (Mor.25), Tunisia (Tun.1) and California 75 (Ca.75). Inoculation technique and readings are similar to the procedure described above. Since no selection in these three cycles has taken plance and at least 75-80 percent homozygosity has been obtained, the frequencies of resistant and suceptible plants, p and q

respectively, may be equal to the initial gene frequency we started with in these populations.

Combining ability analysis

Ten barley cultivars with known and unknown genes for resistance to scald were selected for this study. These parents and their CI numbers are shown in Appendix Table 3. The cultivars were not randomly chosen, but rather selected because of known high attributes for yield, adaptation and scald resistance. Thus, these cultivars will be defined as a population about which inferences will be made.

Crosses were made in the spring of 1980 between the ten parents and all possible combinations except reciprocals. The 45 crosses were grown in Arizona in the winter of 1981 and harvested in April. The F_2 seeds were brought back to Bozeman, MT and were grown along with their parents in a randomized complete block design with two replications at the Horticulture Farm, Bozeman, MT. About 100 seeds were space planted at 6 cm intervals within 6 m rows. A 35 cm spacing was used between the rows. Five plants from each replication were chosen at random and harvested separately and the following measurements recorded:

1. Total yield per plant in grams.
2. Number of seed bearing tillers per plant.
3. Average kernel weight obtained by randomly counting 100 seeds from each plant.

4. Average kernel number per spike was obtained by counting the total number of seeds per plant with an electronic seed counter and dividing by the number of tillers.

Average weather conditions prevailed throughout the growing season. Sprinkler irrigation was utilized a few times to improve infection conditions.

Statistical analysis. Analysis of variance were conducted separately for each character measured in the ten parents and their 45 F_2 progenies for the purpose of detecting true differences among the material. General combining ability effects were analyzed by regression methods.

Chapter 4

EXPERIMENTAL RESULTS

Inheritance of Resistance

The cultivars used in this study, their CI numbers, and their disease reactions to the three isolated of Rhynchosporium secalis used are shown in Appendix Table 1. The Montana isolate (Lew B77) is less virulent than the Tunisian (Tun.1) and the Moroccan (Mor. 25) isolated. The last two isolates appear to possess different genes for virulence as indicated by their reaction to Atlas 46 and Turk (Appendix Table 1). Some of the cultivars used in this study have been tested previously and assigned gene symbols by various workers (Appendix Table 2). The other cultivars such as Steptoe and Gem were selected as parents for this study because of their desirable characteristics and overall performance under a wide range of environmental conditions.

Although such cultivars such as Trebi, Nigrinudum and La Mesita show a susceptible reaction to some isolates of R. secalis they were found to possess one or two recessive gene conditioning resistance (Table 1). Most of the cultivars showed a digenic inheritance (Table 2). The two gene system varied in action according to the parents used. Jet and Steudelli showed two recessive genes as indicated by ratios not significantly different from 3:13 or 1:15. Jet gave a type 0 reaction to the Lew B77 isolate and a type 3 reaction to the Tun.1 and the Mor. 25 isolates. Steudelli was resistant to the Mor. 25

Table 1: Reaction of F_2 plants, resistant or susceptible, to two isolates of *Rhynchosporium secalis* in the progeny of crosses involving Betzes†.

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 1:3	4:12	3:13	7:9
Betzes x Gem (2)*	Tun.1	32	90	.83	.80		
Betzes x Trebi (3)	Tun.1	38	80	.09	.06		.01
Betzes x Atlas (2)	Tun.1	30	106	.49		.26	
Betzes x Nigrinudum (3)	Tun.1	42	94	.14	.10	.00	.00
Betzes x La Mesita (3)	Tun.1	31	111	.44	.54	.28	
Betzes x CI 3940 (0)	Mor.25	39	109	.78			

† Betzes is a susceptible cultivar
* Numbers in parenthesis indicate parent reaction

Table 2. Reaction of F_2 plants, resistant or susceptible, to three isolates of *Rhynchosporium secalis* in the progeny of crosses involving Betzes[†].

Cross	Scald Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 3:13	7:9	1:15	9:7	1:3
Betzes x Steudelli(1-2)*	Lew B77	26	126	.856				.03
Betzes x Steudelli (2)	Tun. 1	45	69		.368			
Betzes x Steudelli (0)	Mor. 25	7	146			.746		
Betzes x Jet (0)	Lew B77	33	153	.997				.03
Betzes x Jet (3)	Tun. 1	22	126	.451				.006
Betzes x Jet (3)	Mor. 25	0	120					
Betzes x Trebi (0)	Lew B77	95	64		.001		.487	
Betzes x CI668 (0)	Lew B77	26	110	.82				.138
Betzes x CI668 (0)	Tun. 1	20	127	.201				.002
Betzes x CI668 (0)	Mor. 25	13	132			.99		
Betzes x Gem (2)	Lew B77	81	78		.09		.116	
Betzes x Gem (2)	Mor. 25	21	131	.216				.002

Table 2. continued

	Scald Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 13:3	3:1	9:7	7:9	1:15	15:1	3:13
Betzes x CI3940 (0)	Lew B77	130	19	.12	.01					
Betzes x CI3940 (0)	Tun. 1	82	29		.87					.04
Betzes x CI4354 (0)	Lew B77	126	26	.86	.03		.00			
Betzes x CI4354 (0)	Tun. 1	110	60			.04	.00			
Betzes x CI4354 (0)	Mor. 25	53	47			.52	.09			
Betzes x W.Hordeum(1)	Lew B77	64	75				.71			
Betzes x W.Hordeum(3)	Tun. 1	7	104					.87		
Betzes x Turk (0)	Lew B77	165	40	.64	.13					
Betzes x Turk (0)	Mor. 25	84	32	.01	.59					
Betzes x Turk (3)	Tun. 1	15	130					.02		.02
Betzes x Kitchin (0)	Lew B77	59	82				.65			
Betzes x La Mesita(0)	Mor. 25	4	109					.47		
Betzes x Atlas 46 (0)	Lew B77	182	24		.01				.01	

†Betzes is a universal susceptible cultivar
*Numbers in parenthesis indicate parental reaction

isolate but intermediate to the other two isolates.

When tested with the Lew B77 isolate the segregation of the F_2 population from Betzes x CI3940 fitted a 13:3 ratio, indicating that a dominant and a recessive gene conditioned resistance of CI3940 (Table 2). The same cross showed one recessive and one dominant to the Mor. 25 and Tun. 1 isolates respectively. The Lew B77 was able to identify both of these genes at the same time. This confirms the hypothesis that resistance of CI3940 is governed by two genes, one dominant, the othr recessive. On the other hand, two dominant genes appear to control resistance in CI4354 as shown by a ratio not significantly different from 9:7.

The segregation of the progeny from crosses involving La Mesita, Forrajera, Bey, Atlas 46 and CI4354 in response to inoculation with the three isolates are presented in Table 3. When crossed with the susceptible cultivars Betzes, Modoc and Trebi, all these resistant varieties gave F_2 segregations compatible with the hypothesis that resistance in each variety was conferred by one or two epistatic dominant genes since significant probability values were obtained based on one or two gene models. Atlas showed an incompletely dominant gene, however, resistance in Nigrinudum may be conditioned by one incompletely dominant gene or two recessive genes (Table 4). The genetic control of resistance in CI668 was examined by crossing this resistant cultivar to Betzes and other susceptible cultivars

Table 3. Reaction of F_2 plants, resistant or susceptible, to three isolates of Rhynchosporium secalis in the progeny of crosses between susceptible x resistant cultivars.

	Scald Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 3:1	12:4	13:3
Betzes x La Mesita	Lew B77	128	60	.02	.02	.000
Betzes x Forrajera	Lew B77	137	47	.932	.78	.01
Betzes x Bey	Lew B77	107	41	.506	.40	.003
Betzes x Atlas 46	Mor. 25	123	36	.552	.672	.156
Modoc x CI4354	Tun. 1	116	37	.924	.900	.059
Trebi x CI4354	Tun. 1	140	46	1.000	.980	.022

Table 4. Reaction of F_2 plants to one isolate of Rhynchosporium secalis in the crosses between susceptible x resistant cultivars.

Cross	Isolate	Resistant (type 0)	Intermediate (type 1-2)	Susceptible (type 3)	Probability 1:2:1
Betzes x Atlas	Lew B77	56	109	48	.704
Betzes x Nigrinudum	Lew B77	61	85	41	.375

(Table 5). The results indicate that resistance in CI668 is controlled by two genes which vary in action depending on the pollen parent used. However, when crossed to Betzes, two recessive genes were detected (Table 2). To further compare these genes with other reported genes in the literature, crosses were made between CI668 with cultivars known to carry specific genes for resistance. Table 6 shows the results of these crosses. In most cases a two gene difference was observed. No susceptible plants were observed in the crosses with Turk, Steudelli, Bey and Nigrinudum. This could be an indication that these cultivars have at least one resistance gene in common, or that the genes of CI668 are closely linked or allelic to the genes of these cultivars. However, susceptible plants were observed in the crosses of CI668 with CI3940, CI4364, Atlas 46, Osiris, Kitchin and La Mesita. This may indicate that the genes of CI668 are different from those of these last six cultivars. The results from the crosses of CI3940 with susceptible cultivars showed dihybrid ratios, except in the cross with Jet where a monohybrid ratio was observed when tested with the Tun.1 isolate (Table 7). To relate the gene system of CI3940 to other known genes for resistance to R. secalis, crosses were made between this cultivar and other resistant lines (Table 8). Since the resistant cultivars CI4354, Trebi, Bey and Turk, when crossed with CI3940, produced F_2 populations that did not segregate for scald reaction, it is evident that the five cultivars carry at

Table 5. Frequency of F_2 plants, resistant or susceptible, to three isolates of *Rhynchosporium secalis* in the progeny of crosses between resistant x susceptible cultivars.

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 13:3	7:9	9:7	15:1	3:13	3:1	12:4
CI668 x Steptoe	Lew B77	67	14	.98					.14	.07
CI668 x Steptoe	Tun. 1	30	34		.75	.14				
CI668 x Steptoe	Mor. 25	72	20	.43					.55	.64
CI668 x Steudelli	Lew B77	74	37			.04				
CI668 x Jet	Lew B77	30	38		.19	.05				
CI668 x Jet	Tun. 1	60	38		.01	.64				.01
CI668 x Jet	Mor. 25	52	28		.01	.17				
CI668 x Atlas	Tun. 1	78	7				.39			
CI668 x Turk	Tun. 1	18	71					.68		
CI668 x Nigrinudum	Tun. 1	85	10				.05			
CI668 x Nigrinudum	Mor. 25	65	13	.87					.12	

Table 5. continued

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 13:3	7:9	1:3	15:1	3:13	3:1	12:4
CI668 x Atlas 46	Tun. 1	68	10	.30					.02	.03
CI668 x La Mesita	Tun. 1	15	57			.50		.64		
CI668 x La Mesita	Mor. 25	53	67		.94					
CI668 x Trebi	Tun. 1	25	48		.12					
CI668 x Trebi	Mor. 25	41	58		.66					
CI668 x Bey	Tun. 1	19	34		.28					
CI668 x Bey	Mor. 25	42	57		.82					
CI668 x Betzes*	Lew B77	26	45		.32					
CI668 x Betzes*	Tun. 1	29	52		.16					

* Reciprocal cross

Table 6. Frequency of F_2 plants, resistant or susceptible, to three isolates of *Rhynchosporium secalis* in the progeny of crosses between resistant x resistant cultivars.

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 13:3	Probability 15:1
CI688 x Turk	Lew B77	132	0		
CI668 x Turk	Mor. 25	112	14	.057	
CI668 x CI3940	Lew B77	112	4		.530
CI668 x CI3940	Tun. 1	71	7		.272
CI668 x CI3940	Mor. 25	115	3		.227
CI668 x CI4354	Tun. 1	73	1		.769
CI668 x CI4354	Lew B77	112	8		.719
CI668 x CI4354	Mor. 25	76	8		.256
CI668 x Atlas 46	Lew B77	180	12	.324	
CI668 x Atlas 46	Mor. 25	50	12	.911	
CI668 x Steudelli	Tun. 1	42	0		

Table 6. continued

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 9:7	13:3	15:1
CI668 x Osiris	Tun. 1	71	12		.486	
CI668 x Osiris	Lew B77	101	4			.585
CI668 x Nigrinudum	Lew B77	103	0			
CI668 x Kitchin	Mor. 25	82	6			.758
CI668 x Trebi	Lew B77	97	0			
CI668 x La Mesita	Lew B77	111	78	.340		
CI668 x Bey	Lew B77	117	0			

Table 7. Frequency of F_2 plants, resistant or susceptible, to three isolates of Rhynchosporium secalis in the progeny of crosses between resistant x susceptible cultivars.

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 13:3	3:1	12:4
CI3940 x Steptoe	Lew B77	152	44	.126		
CI3940 x Steptoe	Tun. 1	152	27	.359		
CI3940 x Steptoe	Mor. 25	138	22	.195		
CI3940 x Nigrinudum	Lew B77	119	18	.171		
CI3940 x Nigrinudum	Mor. 25	98	18	.565		
CI3940 x Jet	Lew B77	127	23	.456		
CI3940 x Jet	Tun. 1	80	38		.089	.062
CI3940 x Jet	Mor. 25	86	21	.755		
CI3940 x Steudelli	Lew B77	85	22	.573		
CI3940 x Turk	Tun. 1	132	24	.456		
CI3940 x Trebi	Tun. 1	112	37		.962	.978
CI3940 x Trebi	Mor. 25	81	29		.419	.713

Table 8. Frequency of F_2 plants, resistant or susceptible, to three isolates of Rhynchosporium secalis in the progeny of crosses between resistant x resistant cultivars.

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 63:1	Probability 15:1
CI3940 x CI4354	Lew B77	105	0		
CI3940 x CI4354	Tun. 1	125	0		
CI3940 x CI4354	Mor. 25	145	0		
CI3940 x Osiris	Lew B77	140	1	.618	
CI3940 x Osiris	Tun. 1	119	10		.353
CI3940 x Trebi	Lew B77	138	0		
CI3940 x Bey	Lew B77	178	0		
CI3940 x Turk	Lew B77	148	0		
CI3940 x Turk	Mor. 25	88	3		.489
CI3940 x Forrajera	Lew B77	132	14		.047

Table 8. continued

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 15:1	63:1	13:3	3:1
CI3940 x Atlas 46	Lew B77	183	13	.590			
CI3940 x Atlas 46	Tun. 1	187	1		.423		
CI3940 x Atlas 46	Mor. 25	116	22			.745	
CI3940 x Steudelli	Tun. 1	118	0				
CI3940 x Steudelli	Mor. 25	59	0				
CI3940 x Gem	Lew B77	192	20	.018			
CI3940 x Forrajera	Lew B77	118	40				1.000
CI3940 x La Mesita	Lew B77	155	26			.240	
CI3940 x Atlas	Lew B77	133	3		.825		

least one gene in common or that close linkage between more than one gene for resistance is involved. The same result was observed in the cross CI3940 x Steudelli when tested with Tun.1 isolate. The remaining crosses segregated in a dihybrid manner.

The results from testing the F_2 populations involving CI4354 with susceptible cultivars are shown in Table 9. Most ratios were digenic except in the cross of CI4354 with Atlas where a monohybrid ratio was observed when tested with the Tun.1 isolate. Crosses were also made between CI4354 and other resistant cultivars (Table 10). All F_2 plants in the crosses of CI4354 with CI3940, Turk, Bey and Trebi were completely resistant. The remaining crosses segregated in a two and three gene difference.

The field studies have revealed few differences in the genetics of resistance of some cultivars to the Lew B77 isolate. There was a significant change in disease reaction of some barley cultivars when evaluation was done under field conditions (Table 11). Since disease rating in the field was done when the plants were maturing it may be possible that the difference observed in the reaction type could be attributed to the adult stage or the environment or their interactions. Trebi and La Mesita which were resistant to the Lew B77 isolate in the greenhouse, showed complete susceptibility under field conditions. Kitchin, Bey, Nigrinudum, Atlas 46, Forrajera, CI668, Modoc and Unitan have changed from resistant to intermediate reaction. However CI3940,

Table 9. Frequency of F_2 plants, resistant or susceptible, to three isolates of *Rhynchosporium secalis* in the progeny of crosses between resistant x susceptible cultivars.

Cross	Isolate	Resistant (type0-2)	Susceptible (type 3)	Probability 13:3	9:7	3:1	7:9	12:4
CI4354 x Unitan	Lew B77	177	26	.067		.000		.002
CI4354 x Unitan	Tun. 1	92	24	.527		.335		.411
CI4354 x Unitan	Mor. 25	120	70		.168	.000		.000
CI4354 x Jet	Tun. 1	119	26	.931		.062		.08
CI4354 x Jet	Mor. 25	97	51		.037			
CI4354 x Atlas	Tun. 1	100	44			.149		.105
CI4354 x Atlas	Mor. 25	85	83		.154			
CI4354 x Steptoe	Tun. 1	122	41			.964		.894
CI4354 x Steptoe	Mor. 25	45	84				.044	

Table 10. Frequency of F_2 plants, resistant or susceptible, to three isolates of Rhynchosporium secalis in the progeny of crosses between resistant x resistant cultivars.

Cross	Isolate	Resistant (type0-2)	Susceptible (type 3)	Probability 15:1	63:1	13:3
CI4354 x Atlas	Lew B77	195	14	.592		
CI4354 x Atlas 46	Lew B77	209	6		.263	
CI4354 x Atlas 46	Mor. 25	129	27			.904
CI4354 x Osiris	Lew B77	178	2		.821	
CI4354 x Osiris	Tun. 1	129	30			.856
CI4354 x CI3940	Lew B77	170	0			
CI4354 x CI3940	Tun. 1	93	0			
CI4354 x CI3940	Mor. 25	121	0			
CI4354 x Turk	Lew B77	136	0			
CI4354 x Turk	Mor. 25	161	15	.126		
CI4354 x Bey	Lew B77	157	0			
CI4354 x Steudelli	Lew B77	132	22			.274
CI4354 x Trebi	Lew B77	185	0			
CI4354 x La Mesita	Lew B77	138	13	.134		

Table 10. continued

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 63:1	15:1	3:1	9:7	13:3
CI4354 x Forrajera	Lew B77	154	2	.998				
CI4354 x Gem	Lew B77	158	14		.177			
CI4354 x Gem	Tun. 1	143	63			.007		
CI4354 x Gem	Mor. 25	100	71				.695	
CI4354 x Nigrinudum	Lew B77	154	22		.274			
CI4354 x Bey	Lew B77	101	25					.673
CI4354 x CI668	Lew B77	83	17					.934
CI4354 x Forrajera	Lew B77	186	0					

Table 11. Disease reaction of 21 barley cultivars to isolate Lew B77 of Rhynchosporium secalis under field and greenhouse conditions.

Cultivar	Disease Rating	
	Greenhouse	Field
Trebi	0	3
Steptoe	3	2
Jet	0-3	2
Kitchin	0	1
Bey	0	2
Nigrinudum	0	1
Atlas 46	0	1
Forrajera	0	2
La Mesita	0	3
CI668	0	1
Gem	2	1
Steudelli	1-2	2
CI3940	0	0
CI4354	0	0
Atlas	0-2	1
Turk	0	0
W. Hordeum	1	1
Betzes	3	2
Osiris	0	0
Modoc	0	2
Unitan	0	2

CI4354, Turk and W. Hordeum did not change in reaction type. The stability of these last four cultivars indicate their potential in breeding programs for scald resistance. It is interesting to note that CI3940 and CI4354 possess resistance to the three isolates used in this study, indicating the possible complexity of the genetic system of resistance in these two cultivars.

Comparisons in the disease reactions of F_2 populations evaluated under greenhouse and field conditions are shown in Tables 12 and 13. In general there is a good agreement between the results obtained under both environments. The F_2 progeny from the cross Betzes x Atlas segregated in a dihybrid manner in the field but showed a monohybrid ratio under greenhouse conditions. The same results were obtained in the cross of Betzes with Nigrunudum. No change in number of genes has been observed in the rest of the crosses but some have shown a change in gene action. For example, under field conditions the F_2 population in the cross of Betzes with Gem segregated according to one dominant gene as shown by a ratio not significantly different from 3:1. However, in the greenhouse this cross showed the presence of two dominant genes as indicated by the 9:7 ratio (Table 12). When resistant x resistant crosses are considered (Table 13), no major change in genetic ratios was noticed. Wherever a difference was observed it could be attributed to the small sample size rated in the field. For

Table 12. Reaction of F_2 plants in the progeny between a susceptible x resistant cultivars to isolate Lew B77 under field (upper values) and greenhouse conditions (lower values).

Cross	Resistant (type 0)	Intermediate (type 1-2)	Susceptible (type 3)	Probability 3:1	9:7	13:3	15:1	1:2:1	1:15
Betzes x Gem	47	0	13	.655					
Betzes x Gem	81	0	78		.116				
Betzes x CI3940	27	0	4			.614			
Betzes x CI3940	130	0	19			.119			
Betzes x Atlas	41	0	4				.503		
Betzes x Atlas	56	109	48					.704	
Betzes x Nigrinudum	4	0	49						.725
Betzes x Nigrinudum	61	85	41					.375	
Betzes x CI4354	28	0	24		.783				
Betzes x CI4354	110	0	60		.042				

Table 13. Frequency of F_2 plants in the progeny between resistant x resistant cultivars to isolate Lew B77 of Rhynchosporium secalis under field (upper values) and greenhouse (lower values) conditions.

Cross	Resistant (type 0-2)	Susceptible (type 3)	Probability 63:1	15:1	13:3
CI3940 x Turk	46	2	.929		
CI3940 x Turk	148	0			
CI3940 x Atlas 46	50	0			
CI3940 x Atlas 46	183	13		.590	
CI4354 x Turk	45	8			.710
CI4354 x Turk	136	1	.638		
CI4354 x Atlas 46	60	1	.397		
CI4354 x Atlas 46	209	6	.263		
CI4354 x Osiris	36	1	.904		
CI4354 x Osiris	178	2	.821		
CI668 x Turk	48	0			
CI668 x Turk	132	0			
CI668 x Osiris	46	0			
CI668 x Osiris	103	4		.585	
CI668 x Atlas 46	39	1	.860		
CI668 x Atlas 46	180	12			.450
CI668 x Nigrinudum	41	0			
CI668 x Nigrinudum	103	0			

example, under field environment all F_2 plants in the cross of CI3940 x Atlas 46 were resistant. Fifty plants may not have been an adequate sample size to detect a two gene difference. When 196 F_2 plants of the cross were evaluated in the greenhouse a dihybrid ratio was observed.

The reaction of F_1 plants to the Mor. 25 isolate from crosses involving Betzes are shown in Table 14. It is interesting to note that in the case of Betzes cytoplasm most of the F_1 plants were susceptible indicating that resistance in these cultivars is conditioned by a recessive genetic system. Only Atlas 46 and Turk show a dominant gene action. All F_1 plants in the cross Betzes x CI4354 were susceptible. This was not expected since it was shown that resistance of CI4354 to the Mor. 25 isolate was dominant (Table 2).

Since resistance to the Mor. 25 isolate was expressed in a recessive manner, it was possible to use the F_1 population from the cross between two resistant cultivars as a test for allelism. Resistant F_1 populations in the crosses of CI3940 with CI4354 and Steudelli were observed (Table 15). This indicates that the recessive genes in each are the same or at least allelic. The F_1 population of the cross CI3940 x La Mesita was susceptible (Table 15), indicating non allelic genes conditioning resistance in both cultivars. Table 16 shows the reaction of F_1 families involving CI4354 and Gem both resistant to the Mor. 25 isolate. The F_1 plants of the cross CI4354 x La Mesita

Table 14. Frequency of F_1 plants, resistant or susceptible, to Mor. 25 isolate of *Rhynchosporium secalis* in the progeny of crosses involving Betzes†

Cross	Resistant (type 0)	Suceptible (type 3)
Betzes x Gem (1)*	0	10
Betzes x CI668 (0)	0	7
Betzes x Jet (3)	0	9
Betzes x Osiris (0)	0	6
Betzes x Steudelli (0)	0	9
Betzes x CI3940 (0)	0	7
Betzes x Atlas (3)	0	9
Betzes x CI4354 (0)	0	14
Betzes x Atlas 46 (0)	6	0
Betzes x Turk (0)	9	0
Betzes x Nigrinudum (3)	0	8
Betzes x La Mesita (0)	0	10

†Betzes is a susceptible cultivar
*Numbers in parenthesis indicate parental reaction

Talbe 15. Frequency of F_1 plants, resistant or susceptible to Mor. 25 isolate of *Rhynchosporium secalis* in the progeny involving CI3940+.

Cross	Resistant (type 0)	Susceptible (type 3)
CI3940 x Steudelli (0)*	6	0
CI3940 x CI4354 (0)	12	0
CI3940 x La Mesita (0)	0	8
CI3940 x Turk (0)	10	0
CI3940 x Atlas 46 (0)	14	0
CI3940 x Jet (3)	7	0

+CI3940 is a resistant cultivar
*Numbers in parenthesis indicate parent reaction

Table 16. Frequency of F_1 plants, resistant or susceptible to Mor. 25 isolate of Rhynchosporium secalis in the progeny involving CI4354 and Gem+.

Cross	Resistant (type 0)	Susceptible (type 3)
CI4354 x Atlas 46 (0)*	14	0
CI4354 X CI3940 (0)	12	0
CI4354 x Turk (0)	13	0
CI4354 x Nigrinudum (3)	12	0
CI4354 x La Mesita (0)	0	10
Gem x CI668 (0)	0	3
Gem x CI3940 (0)	0	8
Gem x CI4354 (0)	0	10
Gem x Atlas 46 (0)	11	0

+CI4354 and Gem are resistant and intermediate cultivars respectively

*Numbers in parenthesis indicate parent reaction

were susceptible indicating that the resistance genes in these two cultivars are different. The resistance genes of Gem also appeared to be different from the genes of CI3940, CI4354 and CI668. As expected, the Gem x Atlas 46 cross produced resistant F_1 plants since resistance of Atlas 46 to the Mor. 25 was shown to be governed by two dominant genes.

Evidence from this research and in the literature suggests that crosses between two susceptible cultivars may produce resistant segregants in the F_2 or later generations. To substantiate this hypothesis with Rhynchosporium secalis, different crosses between susceptible cultivars were made. Tables 17 and 18 show the results of these crosses. It is interesting to note that regardless of the number of genes segregating in these crosses most of them behaved as recessives. Only the Unitan x W. Hordeum cross segregated according to one incompletely dominant gene. W. Hordeum which was resistant to the Lew B77 isolate (Table 2) showed the presence of two recessive genes when crossed to Betzes. As temperature increased to around 27 C in the greenhouse during hot summer days W. Hordeum became completely susceptible. When crossed with Unitan and F_2 plants kept at 27 C W. Hordeum genes still segregated out (Tables 17 and 18).

To further understand and verify the genetics of resistance of some barley cultivars, a backcross involving Betzes was performed. This procedure should reduce the number of plants required to detect

Table 17. Reaction of F_2 plants resistant, intermediate and susceptible to three isolates of Rhynchosporium secalis in the progeny of crosses between susceptible x susceptible cultivars.

Cross	Isolate	Resistant (type 0)	Intermediate (type 1-2)	Susceptible (type 3)	Probability 1:3	1:2:1	3:13	4:12
Steptoe x Unitan	Lew B77	35	0	117	.963		.132	.764
Steptoe x Unitan	Tun. 1	0	16	60	.949		.587	.93
Steptoe x Bey	Mor. 25	0	27	100	.384		.400	.36
Betzes x Nigrinudum	Tun. 1	0	40	94	.138		.005	.170
Betzes x La Mesita	Tun. 1	0	31	111	.438		.281	.920
Betzes x Trebi	Tun. 1	38	0	80	.084		.008	.162
Betzes x Trebi	Mor. 25	0	0	88				
Unitan x W. Hordeum	Lew B77	60	78	52		.503		
Unitan x W. Hordeum	Tun. 1	35	59	35		.632		
Steptoe x Forrajera	Tun. 1	0	40	108	.066		.006	

Table 18. Reaction of F_2 plants in the crosses between susceptible x susceptible cultivars showing a digenic inheritance to three isolates of Rhynchosporium secalis.

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 3:13	1:15	7:9
Betzes x Atlas	Mor. 25	14	112	.058		
Betzes x Unitan	Lew B77	40	135	.116		
Betzes x Unitan	Mor. 25	0	103			
Betzes x Unitan	Tun. 1	10	62	.632		
Betzes x Steptoe	Lew B77	8	103		.561	
Betzes x Steptoe	Mor. 25	3	119		.202	
Betzes x Steptoe	Tun. 1	11	114		.561	
Betzes x Jet	Tun. 1	22	126	.451		
Betzes x Jet	Mor. 25	0	120			
Betzes x Forrajera	Mor. 25	0	136			
Betzes x Forrajera	Tun. 1	9	92		.199	
Betzes x W. Hordeum	Mor. 25	31	65			.026

Table 18. continued

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 3:13	1:15	7:9
Steptoe x Unitan	Mor. 25	9	91		.438	
Steptoe x Forrajera	Mor. 25	14	72	.783		
Unitan x Bey	Tun. 1	14	171		.284	
Unitan x Bey	Mor. 25	9	52	.623		
Bey x Forrajera	Tun. 1	38	148	.443		
Bey x Forrajera	Mor. 25	4	99		.615	

two or three gene segregations. This test was performed with the Mor. 25 isolate of R. secalis only since the number of hybrid seeds was limited. Table 19 shows the results of this experiment. As with the results obtained with the F_1 populations, all ratios indicated recessive resistance. It is interesting to note that in the cross Betzes x CI3940/Betzes only one plant showed a resistant reaction. There was a possible erosion of resistance in Betzes background. This erosion of resistance may be attributed to modifying genes. The results of the backcrosses thus supported the earlier findings and proved that resistance to the Mor. 25 isolate of La Mesita, Nigrinudum, CI4354, Steudelli, CI668 and Gem is conditioned by a recessive gene system.

Reciprocal crosses. The objective of this study was to determine whether cytoplasmic genes for resistance to R. secalis are present in some cultivars. If they exist, breeders can direct their crossing programs accordingly. The disease reaction of F_2 plants resulting from reciprocal crosses are reported in Table 20. In general there were no significant differences between reciprocal crosses to any one isolate. The only difference observed was in the cross Betzes x CI3940 and its reciprocal where a monohybrid and a dihybrid ratios were observed respectively (Table 20).

Table 19. Frequency of F_1 plants, resistant or susceptible to Mor. 25 isolate of *Rhynchosporium secalis* involving a backcross to Betzes+.

Cross	Resistant (type 0)	Susceptible (type 3)	Probability 1:1	1:3	1:7
Betzes x Atlas 46 / Betzes	8	11	.646		
Betzes x La Mesita / Betzes	3	15		.586	
Betzes x Nigrinudum / Betzes	2	12		.381	
Betzes x CI4354 / Betzes	9	17		.365	
Betzes x Atlas / Betzes	0	12			
Betzes x CI3940 / Betzes	1	13			.839
Betzes x Steudelli / Betzes	2	16		.276	
Betzes x Kitchin / Betzes	2	10		.739	
Betzes x Osiris / Betzes	3	12		.882	
Betzes x Jet / Betzes	0	19			
Betzes x CI668 / Betzes	1	14			.769
Betzes x Gem / Betzes	4	12		.773	

+Betzes is a susceptible cultivar

Table 20. Frequency of F_2 plants, resistant or susceptible to three isolates of Rhynchosporium secalis in the progeny of reciprocal crosses.

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 3:13	7:9	13:3	1:3	9:7
Jet x Betzes (3)	Lew B77	27	161	.229				
Betzes x Jet (0)	Lew B77	33	153	.997				
Jet x Betzes (3)	Tun. 1	37	65		.136			
Betzes x Jet (3)	Tun. 1	22	126	.451				
Betzes x CI3940 (0)	Lew B77	140	19			.119		
CI3940 x Betzes (3)	Lew B77	62	63		.251			
Betzes x CI3940 (0)	Tun. 1	82	29			.035		
CI3940 x Betzes (3)	Tun. 1	65	19			.671		
Betzes x CI3940 (0)	Mor. 25	39	109				.776	
CI3940 x Betzes (3)	Mor. 25	58	51					.523
CI4354 x CI3940 (0)	Tun. 1	93	0					
CI3940 x CI4354 (0)	Tun. 1	125	0					

Table 20. continued

Cross	Isolate	Resistant (type 0-2)	Susceptible (type 3)	Probability 9:7	Probability 13:3
CI4354 x CI3940(0)*	Lew B77	170	0		
CI3940 x CI4354(0)	Lew B77	105	0		
CI4354 x CI3940(0)	Mor. 25	121	0		
CI3940 x CI4354(0)	Mor. 25	145	0		
Betzes x CI4354(0)	Tun. 1	110	60	.042	
CI4354 x Betzes(3)	Tun. 1	103	50	.010	
Betzes x CI4354(0)	Mor. 25	53	47	.518	
CI4354 x Betzes(3)	Mor. 25	58	51	.523	
Betzes x CI4354(0)	Lew B77	126	26		.856
CI4354 x Betzes(3)	Lew B77	115	34		.154

*Numbers in parenthesis indicate parent reaction

Recurrent selection population

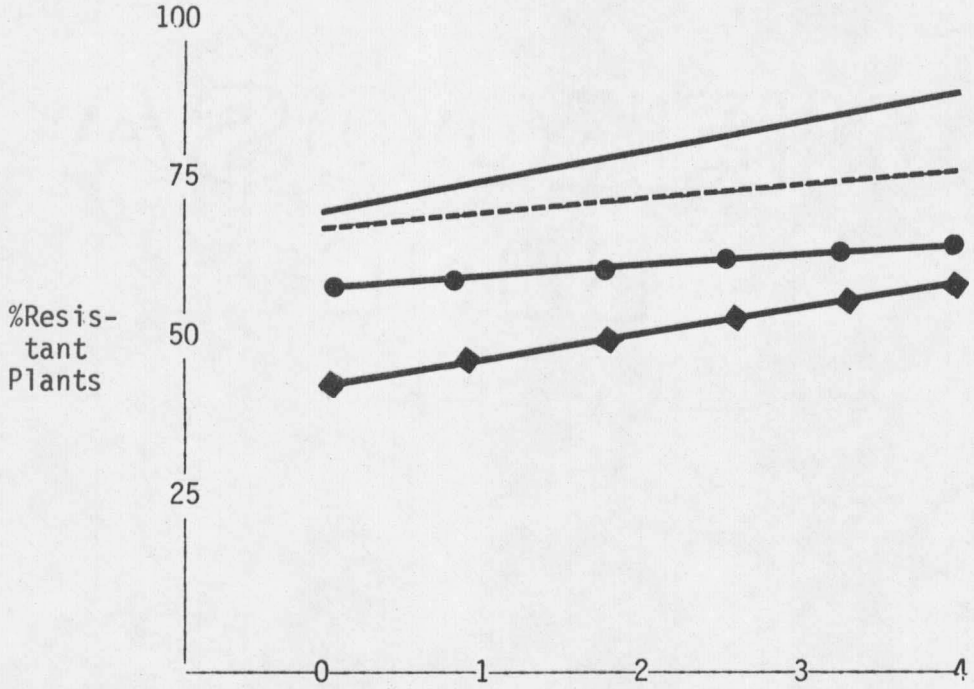
The first objective of this experiment was to measure the change in resistance to scald in the recurrent selection population (RSP-Rrs5) developed by the MSU/USAID barley project. The second objective was to decide whether changes in yield or yield components had occurred in this population when selection was based only on disease reaction. In other words, had there been any erosion in yield in this population? This point is important since in the exploitation of any recurrent selection population developed for disease resistance it is necessary for a breeder to select resistant plants with acceptable yielding ability to be released as a commercial cultivar. It is suggested that resistant plants should not be selected from the population and directly used in a crossing program because of possible loss of the accumulated resistance. Especially this is so if the resistance is conditioned by minor effect genes.

Results. Observed mean squares form the analysis of variance for disease reaction, yield and yield components are presented in Table 21. Significant differences were observed between cycles for all measured traits. To test the response of selection in the different cycles a regression analysis was performed (Fig. 1). To further demonstrate the change in resistance about 200 plants from cycle zero, three and four were selfed for three generations without selection and later inoculated with three isolates of R. secalis. Since no

Table 21. Observed mean squares from reaction type, yield and yield components between cycles of recurrent selection.

Source of variation	Df	Mean Squares				
		Disease reaction	Plant yield	Kernel weight	Kernels/ spike	Tillers/ plant
Blocks	3	12.4**	544.75**	2.12**	788.15**	148.46**
Stages	4	6.99**	1113.53**	19.82	1858.98**	136.48**
Error	12	.84	90.36	.71	174.76	24.56

**Significant at the 1% level



	B	R^2(%)
Lew B77	4.02 (f)	41
Lew B77	2.31 (g)	46
CA 75	1.7*	83
Tun 1	4.4	66

* Significant at the 5% level of probability
g=Greenhouse experiment
f=Field experiment

Figure 1. Response to four cycles of recurrent selection for resistance to three isolates of Rhynchosporium secalis.

selection was practiced and assuming mutations and genetic drift are not important, the percent of resistant plants (p) and percent of susceptible plants (q) are equal to the initial gene frequencies in the population. These results are shown in Table 22. In general there is a good agreement between the results of this experiment with those reported in Table 23. The field experiment (Table 24) also confirmed results obtained in the greenhouse.

The correlation matrix (Table 25) indicated no correlated responses between disease reaction and yield and yield components, but a significant correlation existed between yield and kernels per spike and tillers per plant. Plant yield and kernel weight did not appear to be significantly correlated. Significant negative correlation was observed between kernel weight and kernels per spike. This may be attributed to component compensation.

Regression analysis indicated that when selection in these populations was based solely on disease reaction, there was no significant change in tillers per plant. An increase in kernels per spike and a decrease in seed weight were observed (Table 26). The overall plant yield increased slightly (b = 1.55).

Combining ability analysis

The objective of this study was to estimate the type of gene action controlling yield and yield components of some barley cultivars

Table 22. Frequency of Barley plants resistant (p) and susceptible (q) to three isolates of Rhynchosporium secalis in three cycles of recurrent selection.

	Tun. 1			Ca. 75			Mor. 25		
	p		q	p		q	p		q
Cycle 0	.37±	.034	.63	.34±	.033	.66	.49±	.035	.51
Cycle 2	.66±	.033	.34	.53±	.035	.47	.63±	.034	.37
Cycle 4	.60±	.035	.40	.57±	.035	.43	.60±	.035	.40

Table 23. Frequencies of barley plants resistant and susceptible to three isolates of Rhynchosporium secalis through four cycles of recurrent selection when tested under greenhouse conditions.

	Cycle 0			Cycle 1			Cycle 2			Cycle 3			Cycle 4		
	Isolate			Isolate			Isolate			Isolate			Isolate		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
%Resistant	68	59	41	86	60	44	91	60	55	89	65	62	86	65	54
%Susceptible	32	41	59	14	40	56	10	40	45	11	35	38	14	35	46
SE	.033	.035	.035	.024	.035	.035	.02	.035	.035	.022	.033	.034	.024	.033	.035

Isolate 1 = Lew B77 (from Montana)
Isolate 2 = Ca 75 (from California)
Isolate 3 = Tun 1 (from Tunisia)

Table 24. Frequency of barley plants resistant and susceptible to Rhynchosporium secalis through four cycles of recurrent selection when tested under field conditions with Lew B77 isolate.

	Cycle 0	Cycle 1	Cycle 2	Cycle 3	Cycle 4
% Resistant	68	84	87	94	85
% Susceptible	32	16	13	6	15
S.E.	.033	.026	.023	.05	.025

Table 25. Correlation matrix between five measured traits in the recurrent selection population.

	Plant Yields	Kernel Weight	Kernels/ Spike	Tillers/ Plant
Reaction	-.0995**	-.0145	-.059*	-.0447
Plant Yield		-.0213	.5002**	.6546**
Kernel Weight			-.4398**	-.0155
Kernels/ Spike				-.0155

N = 730

* = Significant at the 5% level

** = Significant at the 1% level

Table 26. Regression coefficients of four measured traits on four cycles of recurrent selection.

	Plant Yield	Kernel Weight	Kernels/ Spike	Tillers/ Plant
b	1.55^{ns}	-8.94*	6.09*	-7.0^{ns}
R^2	5.32%	77.98%	72.63%	.02%

* = Significant at the 5% level

ns = Non significant

that made up the base population of the RSP-Rrs-5. Also to determine if some cultivars were better combiners than others for disease resistance as well as for yield and yield components. Parents with good combining ability are necessary if high yielding plants are to be selected from these populations.

Results. The means for yield and yield components of the parents and their 45 F_2 populations are shown in Table 27. None of the F_2 populations exceeded the parents for all measured traits. Observed mean squares associated with yield and yield components for the ten cultivars and their F_2 hybrid combinations are shown in Table 28. Significant differences were observed in tillers per plant and kernel weight and seeds per head at the 1 percent and the 5 percent level respectively. No significant differences between the entries for yield were observed.

Separate analysis of variance for each character comparing parents to progeny from their crosses as well as general and specific combining ability was computed and the results are shown in Table 29. Parents vs crosses mean squares for kernel weight and tillers per plant were zero. Highly significant difference for plant yield and seeds per head in the parents vs crosses mean squares was observed (Table 29). General combining ability (GCA) mean squares was significant for kernel weight, tillers per plant and seeds per head. Plant yield GCA, however, was not significant. Specific combining ability mean

Table 27. Means for yield and yield components of ten barley cultivars and their 45 F_2 populations.

	Plant Yield(g)	Tillers/ Plant	Kernel Weight(g)	Seeds/ Spike
Parents	23.29	15	4.65	37
F_2	18.91	15	4.66	32

Table 28. Observed mean squares for yield and yield components in ten barley cultivars and their 45 F_2 populations.

Source of Variation	Df	Mean squares			
		Tillers/ Plant	Plant Yield	Kernel Weight	Seeds/ Spike
Blocks	1	1.78	46.26	.19	11.04
Entries	54	24.48**	29.67	.82*	166.85*
Error	54	11.08	27.94	.17	56.46

** and * significant at the 1 and 5% respectively

Table 29. Observed mean squares associated with general and specific combining ability for yield and yield components in ten barley cultivars and their 45 F_2 populations.

Source of variation	Df	Mean squares			
		Kernel Weight	Tillers/ Plants	Plant Yield	Seeds/ Spike
Blocks	1	.221	.893	54.87	12.79
Entries	54	.83**	24.50**	29.67	176.10
Among parents	9	.67**	1.68*	29.38	185.60**
Parents vs crosses	1	.00	.00	300.00**	400.00**
Crosses	44				
GCA	9	1.53**	8.09**	37.78	382.2**
SCA	35	.70**	9.59	19.93	114.4**
Error	54	.17	11.24	28.04	56.40

*, ** significant at the 5 and 1% respectively

squares was significant for kernel weight and seeds per head only.

General combining ability effects for disease reactions, yield and yield components for 10 barley cultivars used in the diallel experiment are shown in Table 30. Negative effects for disease reaction indicate good combining ability of that parental cultivar, but negative effects for yield and yield components are an indication of poor combining ability. Cultivars CI668, CI3940 and CI4354 had negative GCA effects for disease reaction to the three isolates. Gem, which has an intermediate reaction to all isolated of R. secalis, was found in general to be a good combiner for disease resistance, yield, kernel weight and tillers per plant. This cultivar is almost ideal to be included in this population. Betzes, a susceptible cultivar to all isolates, as expected, had positive effects to the three isolates. Steptoe, also a susceptible cultivar, was found to have positive effects for disease reaction and negative effects for yield, kernel weight and tillers per plant. On the other hand, Forrajero had positive effects in regard to disease reaction to the three isolates, as well as yield and yield component.

Table 30. General combining ability effects of 10 barley cultivars for yield, yield components and disease reaction to three isolates of Rhynchosporium secalis.

Parents	Isolate Lew B77	Tun.1	Mor.25	Plant Yield	100 Kernel weight	Tillers per plant	Seeds/ heads
CI668	-.32	-.32	-.3	-.296	.637	1.75	-7.42
CI3940	-.46	-1.2	-1.13	-.86	-.39	-2.06	4.64
CI4354	-.23	-.98	-.48	.407	-1.67	2.81	4.63
Betzes	.92	.73	.73	-.861	.185	4.25	-7.11
Gem	-.36	-.002	-.2	2.158	.195	.375	-.297
Steptoe	.53	.46	.22	-3.3	-.381	-2.5	5.95
Unitan	-.35	-.03	.16	1.59	-.148	-.188	2.13
Bey	.33	.53	.31	-.078	.052	-1.82	1.89
Forrajera	.24	.49	.49	1.47	.149	.125	.015
W.Hordeum	-.30	.33	.20	-2.44	.137	-1.05	4.83
				S.E=.46	S.E=.09	S.E=.21	S.E=1.47

Chapter 5

DISCUSSION

The main objective of any breeding program is the production of new cultivars that possess greater potential than those already under cultivation. To reach this objective with a minimum of time and expense, the breeder must have some familiarity with the inheritance of different traits in a crossing nursery.

Genetic information about different sources of resistant germplasm is a prerequisite for an effective breeding program for the development of scald resistant cultivars.

In this study an attempt was undertaken to gain more understanding of some barley cultivars that made up the recurrent selection population for scald resistance in terms of disease resistance and combining ability.

The results obtained from crosses involving Betzes, a susceptible parent to the three isolated used in this study, suggested that resistance in Jet and Steudelli was conditioned by two recessive genes. This is in agreement with the findings of Baker and Larter (1963) who first reported the presence of these two complementary recessive genes. Baker and Larter (1963) designated these genes are rh6 and rh7. They further observed the sensitivity of these two genes to increased temperatures. This was confirmed in the present study. Following some warm days when temperature in the greenhouse reached 27 C these

two cultivars showed a complete susceptible reaction. The same phenomenon was observed for the cultivars La Mesita, W. Hordeum and Nigrinudum. It is interesting to note that all these cultivars possess recessive genes for resistance. Bockelman et al. (1977) found that the rh6 and rh7 are on chromosome 4 and 3 respectively. Hapgood and Hayes (1971) presumed the rh7 to be an allele of the Rh-Rh3-Rh4 locus complex. The change in disease reaction as affected by temperature has been reported for the Sr6 gene conditioning resistance to Stem rust (Puccinia graminis tritici). At high temperature the Sr6 gene shows a susceptible reaction, but at lower temperature it conditions a resistant reaction (Bromfield, 1961). Since Jet, Steudelli, W. Hordeum and Nigrinudum possess temperature sensitive genes, their usefulness in breeding programs is limited and perhaps should not be included as components of the recurrent selection population, unless they possess different temperature sensitive genes.

The two cultivars Forrajera and Bey were shown to have a single dominant gene for resistance to R. secalis. Bey was shown by Wells and Skoropad (1963) to contain one dominant gene designated Rh3. Since Forrajera and Bey behaved similarly to the three isolates, it was assumed that Forrajers also possesses the Rh3 gene or a gene closely linked to it. This was also suggested by the absence of susceptible segregates in the cross between Bey and Forrajera. An examination of the segregation ratios obtained in the crosses of these two

cultivars with CI3940 and CI4354 indicated that the genes in Bey and Forrajera were not the same but allelic or closely linked. Dyck and Schaller (1961) reported on the close linkage between the Rh3 and the Rh4 genes.

La Mesita and Atlas 46 appeared to possess different genes for resistance. Atlas 46 was resistant to the Mor.25 isolate, but La Mesita showed an intermediate reaction to this same isolate. Atlas 46 was derived from a backcross to Turk. The initial cross was performed in order to incorporate scale resistance from Turk into Atlas. The present study revealed that Atlas 46 has two dominant and one recessive genes for resistance. The recessive gene in Atlas 46 had not been reported in the literature but was not unexpected. Since Atlas 46 is a derivative of Turk and since the present results indicated that resistance in Turk was also conditioned by two dominant and one recessive gene (Rh5 Rh rh6) it is thus logical to assume that the recessive gene in Turk was carried into Atlas 46. The other two dominant genes are possibly the Rh2 gene from Atlas and the Rh5 from Turk. Habgood and Hayes (1971) found that Turk has one dominant and one recessive gene which they designated as Rh rh6. The same authors, however, reported that Atlas 46 has only one dominant gene. On the other hand, Dyck and Schaller (1961) and Starling et al. (1969) showed that resistance in Atlas 46 is conditioned by two dominant genes. It is thus assumed that the genes in Atlas 46 are the Rh2

Rh5 rh6. The findings of the present study further demonstrated that Atlas had two dominant genes in terms of the Lew B77 isolate. The first gene is incompletely dominant and conditioned resistance in the seedling stage the second gene conditioned resistance in the adult stage. The same phenomenon was observed for the cultivar Nigrinudum which showed one incompletely dominant gene in the greenhouse and two recessive genes in the field. Moseman (1966) reported that four genes in wheat (Triticum aestivum spp vulgare (vill., Host) tritici) conditioned resistance to the powdery mildew fungus in the seedling stage. Two different genes were effective only in the adult stage. Sharp (1973) reported that the genes Sr2, Sr3 and Sr4 in stem rust conditioned only mature plant resistance to stem rust of wheat (Puccinia graminis tritici) while the other Sr genes were effective in the seedling stage. Dyck and Schaller (1961) reported that resistance in Atlas was governed by a single dominant gene designated Rh2. The second gene reported in this study had not been previously reported in the literature. Since Dyck and Schaller (1961) studied only seedling reaction of crosses involving Atlas, it is not surprising that they did not detect this additional gene.

The inheritance of La Mesita was found to be controlled by two recessive temperature sensitive gene pairs in terms of the Mor. 25 isolate. The F_1 plants of Betzes x La Mesita were susceptible to the Mor. 25 isolate of R. secalis. La Mesita showed an additional single

dominant gene to the Lew B77 isolate. This dominant gene is probably the same as the Rh10 described by Habgood and Hayes (1971). The two recessive genes found in La Mesita in the present study have not been described previously and did not appear to be in the Rh-Rh3-Rh4 locus complex. Riddle and Briggs (1950) also reported the presence of one dominant gene in La Mesita; however, Habgood and Hayes (1971) found two dominant genes conditioning resistance in this cultivar.

The backcross analysis indicated that both Nigrinudum and Osiris had two recessive genes each in terms of the Mor. 25 isolate. This was further confirmed by the reaction of F_1 plants resulting from the crosses between these cultivars with Betzes. Baker and Larter (1963) reported that Nigrinudum had one recessive gene designated rh8 but failed to test its allelic relationship to the rh6 and rh7. Habgood and Hayes (1971) found three genes in Osiris, two dominant and one recessive, which they designated Rh4, Rh10 rh6.

The genetics of resistance of the cultivars Gem, CI3940 and CI4354 had not been previously investigated. Gem appeared to have two recessive genes in terms of the Lew B77 isolate. Gem had shown an intermediate reaction to the three isolated of R. secalis used in this study, while CI3940 and CI4354 were resistant to all isolates. This may be an indication that the gene system in Gem is different from that in CI4354 and CI3940. Furthermore, susceptible segregates were observed in the crosses of Gem with both of these cultivars.

Cultivar CI4354 showed the presence of two complementary dominant genes to the Tun. 1 isolate. The two genes must be present in order for resistance to be expressed. When tested with the Lew B77 isolate one dominant and one recessive gene were observed. However, two recessive genes segregated to the Mor.25 isolate. This change in gene action cannot be explained in simple Mendelian genetics. Since the reaction of F_2 plants resulting from the cross CI4354 x Betzes was identical to the three isolates, it is possible that the same genes were involved but change in gene action depending on the isolate used. The resistance of CI3940 to the Mor. 25 isolate was conditioned by a single recessive gene; however, a second dominant gene was identified when the F_2 plants of CI3940 x Betzes were tested with the Tun. 1. The Lew B77 isolate was able to detect both of these genes. Comparisons were made between the gene system of resistance in CI3940 and CI4354 with other known genes for resistance to R. secalis. In the cross between these two cultivars no susceptible F_2 plants were observed. This indicated that the dominant genes in each cultivar are the same or closely linked. It was further observed that in the crosses involving these two cultivars with Bey, Turk, Trebi and Steudelli all F_2 plants were resistant. This may indicate an allelic relationship or close linkage between the genes in these cultivars and the genes in both CI3940 and CI4354. Wells and Skoropad (1963) found the Rh3 gene in Bey. Turk genes were designated Rh rh6 by Habgood and

Hayes (1971) and Rh3 Rh5 by Dyck and Schaller (1961). As was reported earlier, Steudelli genes were designated rh6 rh7 by Baker and Larter (1963). It was assumed that the recessive gene in CI3940 is the rh6 or a gene closely linked to it. Furthermore, the dominant gene in both CI3940 and CI4354 conditioning resistance to the Lew B77 and Tun.1 isolate appeared to be the same or allelic to the Rh-Rh3-Rh4 gene complex. Neither one of these cultivars had the Rh2 or the Rh10 genes because susceptible segregates were obtained in the crosses between these cultivars with Atlas (Rh2) and La Mesita (Rh10). All F_2 plants in the crosses involving Turk and CI3940 and CI4354 were resistant, further supporting the hypothesis that the Rh gene is allelic or closely linked to the dominant genes in both of these cultivars. The second gene in CI4354 appeared to be new and is not allelic to the Rh, Rh3, Rh4 or Rh2. However, the recessive gene of CI3940 was believed to be the rh6.

The evidence presented so far indicates that the gene system in CI4354 and CI3940 may be conditioned by a dominant gene at the Rh-Rh3-Rh4 locus complex. It is interesting to note that this locus was found to be the predominating one in 32 barley cultivars studied by Starling et al. (1971). Most of the cultivars studied so far in the literature appeared to have one gene at this complex locus.

The resistance of Gem appeared to be different than that of CI3940 and CI4354. Two complementary dominant genes controlled

resistance in Gem which differed from the Rh3, Rh, Rh4 genes. This was further supported by the observation of susceptible segregates in the crosses between Gem and Bey (Rh3), Forrajera (Rh4) and CI3940 (Rh rh6).

Baker and Larter (1963) reported that resistance in Kitchen and CI668 was controlled by a single incompletely dominant gene designated Rh9. Rh9 was found on chromosome 4 (Bockelman et al., 1977). In the present study this gene was not observed, but rather two recessive genes were found. It was interesting to note that in Betzes cytoplasm, CI668 genes behaved as recessives but changed to some type of dominance in its own cytoplasm. This change in gene behavior was not due to reciprocal differences (cytoplasmic genes) since the Betzes x CI668 and its reciprocal segregated in the same manner. It thus appeared that the change in gene action was due to genetic background rather than cytoplasmic genes. Ramage (1980) reported that the character expression of a gene can be modified by changing the genetic background of the gene. This change in gene action is similar to the observation made earlier with cultivar CI4354, which was referred to as reversal of dominance by Ali (1975a). No susceptible plants were observed in the crosses of CI668 with Turk (Rh rh6), Stuedelli (rh6 rh7), Nigrinudum (rh8) and Bey (Rh3). This indicated again allelic relationship or close linkage of these genes with those of CI668.

The results of the F_1 and backcross analysis supported the

conclusions made so far. The only exception was cultivar CI4354 where a change in gene action was observed. Resistance in Gem, CI668, Osiris, Steudelli, CI3940, CI4354 and La Mesita appeared to be recessive since F_1 plants when inoculated with the Mor. 25 isolate were all susceptible. When resistance is expressed as recessive, it is then possible to use the F_1 data as a test of allelism. Resistant F_1 plants indicate allelic relationship; however, a susceptible F_1 may be a proof of non-allelic genes. When Gem was crossed with CI668, CI3940, CI4354, all plants were suceptible. This again supported the earlier conclusions that different loci may control resistance in Gem and the other three cultivars. Resistant F_1 plants were obtained in the crosses of CI3940 with Steudelli and CI4354 indicating allelic relationship. Resistance of La Mesita appeared to be independent of that of CI4354 and CI3940. Furthermore, the results obtained in these studies indicated the presence of at least five alleles at the Rh locus; one recessive (rh7), one incompletely dominant (Rh8) and three dominant (Rh, Rh3 Rh4) alleles. Habgood and Hayes (1971) have also reported five alleles at the Rh locus (Rh, Rh^2, Rh3, Rh4, rh7). The phenomenon of multiple allelism has been reported in several host-pathogen systems. Moseman (1966) reviewing the genetics of powdery mildew in barley reported five alleles at the Mla locus complex. These alleles were found on chromosome 3. The Rpl locus conditioning rust resistance in Maize was found to have 13 alleles (Saxena and Hooker, 1964). Two and five

alleles for stem rust resistance were found at the Sr7, Sr9 loci respectively (Loegering and Sears, 1966). The best example of multiple allelism has been reported by Flor (1942). He found 11, 6, 3, 4 and 2 alleles at the L, M, N, P and K loci, respectively, conditioning resistance of the flax (Linum usitatissimum L.) to the flax rust pathogen Melampsora Lini (Ehrenb.) Lev. It is difficult in most genetic studies to confirm any one model, especially when the F_2 data can fit a monohybrid and a dihybrid at the same time. Thus interpretation of such ratios can be misleading and cannot be confirmed.

The summary of the genes for resistance in the cultivars examined in this study are summarized in Appendix Table 4.

Traditionally plant breeders have transferred major gene resistance from wild or close relatives of either wheat or barley by backcrossing to a recurrent parent with desirable characteristics. This procedure, however, may take few generations and usually the donor parents are poor combiners or possess bad traits and sometimes the desirable traits are not recovered due to masking. A good example of genetic resistance to stripe rust associated with unacceptable agronomic characters is displayed by the wheat cultivar CII78383. Recently evidence was presented that susceptible parents with good agronomic traits may be combined with a parent that has a complementary genetic background to give usable resistance (Krupinsky and Sharp, 1979). These factors termed minor effect genes, were shown

to be polygenically inherited to segregate in a transgressive manner to have an additive effect and usually condition race-non specific resistance. There is a wide acceptance that minor effect genes are the most genetic basis of horizontal resistance as advocated by VanderPlank (1968). In the present work, crosses between two cultivars susceptible to R. secalis indicated the presence of one or two factors for resistance. These factors behaved in all cases as recessives. It was interesting to note that in the seventeen crosses performed between susceptible cultivars, only four crosses showed no segregation for resistance, five showed segregates in the intermediate reaction and the remaining crosses indicated transgressive segregation for resistance. Thus, it was concluded that not all susceptible cultivars possess resistance factors, but the majority do indeed carry some type of resistance factors. The expression and the penetrance of these genes depends largely on the genetic background of the parents used in the cross. Polygenic inheritance usually shows transgressive segregation. Hooker (1967) failed to detect transgressive segregation for resistance to corn rust (Puccinia sorghi Schw.). Scharen and Bryan (1979) found transgressive segregation for resistance to Septoria nordorum in spring wheat. Recently Bordelon (1981) found evidence for transgressive segregation toward greater resistance to net blotch in crosses between susceptible cultivars with no major genes for resistance.

The fact that susceptible cultivars may contain some genetic factors for resistance, which are not detectable in the parent "per se" holds great promise. It is possible that ancient overcome major genes may constitute what is now known as minor effect genes. If this is the case then recycling of these factors may prove useful in breeding programs. It thus becomes worthwhile for breeders to recombine susceptible commercial cultivars in anticipation of obtaining usable resistance via transgressive segregation. The evidence in the present study indicated that resistance of barley to R. secalis was controlled by chromosomal genes with various action and possibly with some sort of gene interaction. In all reciprocal crosses studies only one cross showed a significant difference. Cultivar Betzes x CI3940 segregated according to one regressive gene in terms of the Mor. 25 isolate, but the reciprocal cross showed the presence of two complementary genes. This same cross behaved in the opposite manner to the Lew B77 isolate. One dominant and one recessive gene were observed when Betzes was used as the female parent. It thus appeared that detection of cytoplasmic genes is associated with the isolate used. The gene-for-gene hypothesis holds for extrachromosomal genes as well. In any case it appeared that most efficient use of the resistant genes of CI3940 should be directed in using this cultivar as the female parent. Since CI3940 is a component of the recurrent selection population for scald resistance, a male sterile gene should

be incorporated in this cultivar.

Bryner (1957) studied the inheritance of resistance to scald in the cross Brier x Wong and its reciprocal and found no differences. Since he studied only one cross, a general statement negating the presence of cytoplasmic genes for resistance to scald in barley can not be substantiated. Extrachromosomal factors have been shown for crown rust resistance in oats (Johnson et al., 1967). Another sensational example of cytoplasmic genes was depicted by the southern corn leaf blight epidemic of 1970. The cytoplasm was shown to be susceptible to Helminthosporium maydis and this susceptibility was associated with the mitochrondia.

The main objective for the development of recurrent selection population for scald resistance was first to incorporate different genes for resistance to scald into a population. The multigenic resistance would represent an approach for avoiding the "boom and bust" cycle especially with variable pathogens such as R. secalis. The selected plants, in addition to their broad based resistance should have desirable agronomic traits and possess an acceptable yielding capacity to be released as a commercial cultivar.

The results of the present study indicated that there was a slow build-up of resistance to the three isolates after four cycles of recurrent selection although regression analysis indicated no significant increase in resistance except to the Ca. 75 isolate. This may be

due to several things. First, since multiple allelism for resistance have been observed in some component cultivars of the recurrent selection population, it is difficult to combine these alleles into any single genotype. The little increase observed in these populations may be due to the accumulation of the few independent genes. Further, since random mating is rare, it may take a few generations to observe any significant increase in resistance. Multiple alleles represent a disadvantage for accumulating different genes for resistance, not only in the recurrent selection method but to conventional breeding programs as well, since only one allele can be present at one time in a homozygous line. The use of multiline cultivars could circumvent this disadvantage. The second reason for the non-significant increase in resistance may be attributed to the lack of sufficient disease incidence with each isolate at each cycle at different disease nurseries. This, however, was not the case with the Lew B77 isolate. At Bozeman, Montana artificial inoculation was performed every year and good infection was obtained. In some nurseries selection was based on agronomic traits due to insufficient or absence of nature infection. The small increase in resistance was also proven by the little change in plant frequencies as shown by the p and q values. The selfing experiment demonstrated a significant increase in resistance to the Tun. 1 isolate but a slow change in resistance to the Mor. 25 isolate. It is interesting to note that a decline in percent resistant plants

was observed in the last cycles to the Tun. 1, Mor. 25 and Lew B77 isolates. If resistance is dominant, then it is difficult to eliminate the susceptible allele, thus susceptible plants are expected after each cycle of recombination. Once a recurrent selection population is developed to about 80 percent resistance as is the one described, the matter of gene deployment is of critical interest. Furthermore, it appears that new selection schemes must be adopted to improve the population agronomically and to exploit it efficiently in the future. For example, a breeder may use this population to establish a "poly-multi-line". Plants in this population should on the average possess more than one gene for resistance to scald. Male Sterile Facilitated Recurrent Selection should have aided in achieving the accumulation of different genes for resistance in each plant. If this is the case, then this population should be ideal for the development of a polymulti-line, each line possessing more than one gene for resistance instead of the usual one gene difference, hence it could be termed a polygenic multi-line or polymulti-line. Plants with similar appearances in height, maturity and seed color are harvested and bulked. Polymulti-line breeding, if property conceived and organized, may have great flexibility and advantages over the usual multi-line breeding. Life expectancy of resistance in components with more than one gene for resistance is probably longer than cultivars with only one gene.

Also, backcrossing may not be necessary to recover isolines sufficiently alike for use in multi-line cultivars. It is possible that phenotypically similar plants with different genes for resistance may already exist in this population. Polymulti-line should also circumvent the disadvantage of multiple alleles.

It was assumed that the main reason for the insignificant built-up of resistance was probably due to the small number of independent genes conditioning resistance to scald. It was clearly demonstrated in the present study as well as in the literature that the Rh-Rh3-Rh4 locus complex is the predominating one in the majority of the cultivars studied so far. From a breeders' point of view the probabilities of selecting resistant plants in these populations appeared to be adequate. However, since disease resistance and yield did not appear to be correlated in these populations, a breeder should select for resistance and high yield simultaneously. Regression analysis further indicated that in the absence of selection for yield or yield components, there was no change in tillers per plant. There was, however, an increase and a decrease in kernels per spike and seed weight respectively. This may be attributed to component compensation. It was obvious that natural selection favors plants that produce a large number of seeds. To maintain a good kernel weight, a breeder should sieve out smaller kernels and keep selecting for good agronomic traits important in his region such as plant height, maturity date, etc.

The diallel analysis indicated that non-additive gene action is important for kernel weight and seeds per head as was shown by the significance observed in the specific combining ability. Additive gene action was important for tillers per plant and kernel weight. Additive genetic variance is important to the breeder of self-pollinated crops since it is fixable in later generations. Thus it is suggested that in the recurrent selection population breeders should select for higher tiller number and kernel weight.

Under ideal conditions, a component cultivar in the recurrent selection population should in addition to its disease resistance be a good combiner for yield. The results of this study indicated that CI668, CI3940 CI4354, Gem and Unitan were good combiners for disease resistance as indicated by their negative GCA effects. Gem and CI4354 appeared to be good combiners for yield and yield components. Cultivars of this type constitute ideal components of the recurrent selection population. However, CI668, Betzes, Steptoe and W. Hordeum on the average do not contribute significantly to their progeny in terms of yield. From the ten cultivars studied for combining ability, only three appeared to be good combiners with regards to yield and disease resistance, the remaining were poor. This is perhaps why the plants in the recurrent selection population in general are not very attractive in terms of good agronomic appearance.

Chapter 6

SUMMARY AND CONCLUSIONS

Genetic studies pertaining to the identification of a gene locus and its relationship to other gene loci depend largely on the gene action of the particular gene, the environment and the interaction between the gene and its environment. It has been shown clearly in this study that expression of resistance genes in some cultivars is related to the ambiant temperature. Thus the interpretations of genetic results become more difficult to discuss in terms of Mendelian genetics. Ali (1972), Jackson and Webster (1976) also found considerable influence of invironmental conditions on symptom expression. The author drew attention to the different interpretations that would reult depending on how the plant reacted at the time of disease rating.

The present study revealed that the number of genes governing resistance to scald may be small and that most of them are located at the Rh-Rh3-Rh4 complex locus on chromosome 3. Furthermore, a multiple allelic series or a tight linkage may exist at this locus. The mode of action of these genes is variable due to various causes including their sensitivity to the environment and especially the genetic background to which they are introduced. The effect of the genetic background was most evident when one resistant cultivar was crossed with the two susceptible parents and the resulting segregating F_2

population evaluated with the same isolate. Results in this study further indicated the presence of minor effect genes for resistance not expressed in the parent "per se" but evident when the susceptible cultivar is crossed with another susceptible cultivar possessing the appropriate background or the complementary factors needed for the expression of the "silent" gene. It is possible that the susceptible parents manifesting transgressive segregants are heterozygous for some loci conditioning resistance. The resistance is expressed as a recessive character and is probably masked by the dominant allele conditioning susceptibility in the parent itself. This possibility is remote but can not be excluded. The occurrence of minor effect genes in commercially acceptable cultivars is of major importance in breeding programs for disease resistance. Identification of resistance factors depends on the virulence genes present in the pathogen. It is thus possible that additional resistance genes are present in any one cultivar.

If genes for resistance are inherited independently, then recurrent selection can be an effective tool for pyramiding different resistance factors in single lines. There was no significant built up of resistance to R. secalis in the recurrent selection population (Rrs-5) probably due to the small number of genes conditioning resistance or to inefficient selections. However, the probability of selecting a

resistant plant from the population remains high since on the average about 80 percent of the plants are resistant.

No significant correlation between disease reaction and yield or yield components existed in the Rrs-5 population. A breeder may therefore select for high yield and resistance simulataneously. Selection for kernel weight is probably effective since additive gene action is predominantly involved in the expression of this trait.

Combininb ability analysis indicated that only three of the ten cultivars evaluated appeared to be combiners for yield or yield components. This is perhaps the reason for the poor agronomic appearance of some plants in the recurrent selection population.

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APPENDIX

Appendix Table 1. Barley cultivars used in this study and their reactions to three isolates of Rhynchosporium secalis.

Cultivar	CI	Isolate Lew B77	Mor. 25	Tun. 1
Gem	7243	I	I	R-I
Unitan	10421	R	I	R
Steptoe	15229	S	S	S
Betzes	6398	S	S	S
Abyssinian	668	R	I	R
Abyssinian	3940	R	R	R
Abyssinian 5	4354	R	R	R
Altan	4118	I	S	I
Atlas 46	7323	R	R	S
Turk	14400	R	R	S
La Mesita	7565	R	R	S
Modoc	7566	R	S	S
Jet	967	R	S-R	S
Nigrinudum	11549	R	S	S
Osiris	1622	R	I	R
Trebi	963	R	S	S
Kitchin	1296	R	I	S
Bey	5581	R	S-R	S
Steudelli	2226	R	S	I
Forrajera	8158	R	S	S
W. Hordeum 801/60 Ragusa 420	11839	I	S	S

Appendix Table 2. Barley cultivars used in this study and their designated genes conferring resistance to Rhynchosporium secalis.

Cultivar	CI	Gene Symbol	References
Abyssinian	668	Rh9	Baker and Larter (1963)
Atlas	4118	Rh2	Dyck and Schaller (1961)
Atlas 46	7323	Rh2 Rh3	Dyck and Schaller (1961)
La Mesita	7565	Rh4	Dyck and Schaller (1961)
		Rh4 Rh10	Habgood and Hayes (1971)
Modoc	7566	Rh4	Dyck and Schaller (1961)
		Rh rh6	Habgood and Hayes (1971)
Nigrinudum	2222	rh	Riddle and Briggs (1950)
		rh8	Habgood and Hayes (1971)
			Wells and Skoropad (1963)
Osiris	1622	Rh4	Dyck and Schaller (1961)
		Rh3	Wells and Skoropad (1963)
		Rh rh6 Rh10	Habgood and Hayes (1971)
Steudelli	2266	rh6 rh7	Baker and Larter (1963)
Turk	5622	Rh3 Rh5	Dyck and Schaller (1963)
		Rh3	Wells and Skoropad (1963)
		Rh rh6	Habgood and Hayes (1971)
Jet	967	rh6 rh7	Baker and Larter (1963)
Kitchin	1296	Rh9	Baker and Larter (1963)
Trebi	936	Rh4, Rh3 Rh4	Starling et al. (1971)
		rh	Riddle and Briggs (1950)
Bey	5581	Rh3	Wells and Skoropad (1963)

Appendix Table 3. Barley cultivars used in the Diallel experiment.

Cultivar	CI Number
Abyssinian	668
Abyssinian	3940
Abyssinian 5	4354
Betzes	6398
Gem	7243
Steptoe	15229
Unitan	10421
Bey	5581
Forrajera	8158
W. Hordeum 801/60 Ragusa 420	11839

Appendix Table 4. Observed and reported genes conditioning resistance to Rhynchosporium secalis in some barley cultivars.

	Tun.1	Mor.25	Lew B77	Literature
Gem	rh	rhrh	rhrh	
Atlas	rh		Rh2*Rh	Rh2
CI3940	Rh	rh6	Rhrh6	
CI4354	RhRh	rhrh	Rhrh	
La Mesita		rh6rh7	Rh10	Rh4,Rh4Rh10
Forrajera			Rh4	
Bey			Rh3	Rh3
Atlas 46	Rh5	Rh5	Rh2Rh3	
			Rh2rh6	Rh,Rh2Rh3
Nigrinudum		rhrh	rhRh8*	rh8
Steudelli	rh6rh7	rh6rh7	rh6rh7	rh6rh7
Jet	rh6rh7	rh6rh7	rh6rh7	rh6rh7
Trebi			Rh4Rh	Rh4,Rhrh6
W.Hordeum			rh6rh7	
Kitchin			rhrh	Rh9
CI668	rh6rh7	rh6rh7	rh6rh7	Rh9
Turk		Rh5	Rh3	
			Rh3rh6	Rh3Rh5

* Incompletely dominant gene

Harrabi, M. M.
The inheritance of resistance of Barley

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