



Conservation of powdery mildew resistance genes in three composite cross populations of barley
by Guy De Smet

A thesis submitted in partial fulfillment of the requirements for the degree of DOCTOR OF
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Abstract:

The barley *Erysiphe graminis* f.sp. *hordei* host-parasite system was used as a model to evaluate the potential of barley composite cross populations for conservation of disease resistance. The objective was to determine if increases in resistance to powdery mildew could be detected over periods of time in composite cross populations developed in California, where the disease might have had a selective influence on the populations, and the same populations grown in Montana, where no selective influence of powdery mildew was expected. Four isolates of *E. graminis* f.sp. *hordei* were used to monitor the frequencies of specific mildew resistances through early, intermediate and late generations of three composite cross populations (CC II, CC V, CC XII) grown at Davis, California, and Bozeman and Moccasin, Montana.

Following artificial inoculation with the powdery mildew cultures in a controlled environment, the barley seedlings were classified as resistant or susceptible according to their reaction types. The number of resistant seedlings was computed for each treatment combination in each replication and converted to a percentage form, on which statistical analyses were performed.

Changes in frequencies of plants resistant to the four isolates were observed between generations in all populations from the three locations. Increases in the frequency of resistant plants were detected by inoculations with culture 59.11 in CC II from Bozeman and CC XII from Bozeman and Moccasin, and by inoculations with cultures 63.12 and MT from the California CC XII. The largest increases in frequency of resistance were detected by inoculations with culture 59.11. CC XII revealed the most and largest increases in resistance of the three barley populations. Trends in the frequencies of resistance are discussed in relation to selection pressure applied by powdery mildew. It is suggested that associations with gene complexes other than resistance to *E. graminis* might help to explain the increased resistance observed in these studies.

CONSERVATION OF POWDERY MILDEW RESISTANCE GENES IN
THREE COMPOSITE CROSS POPULATIONS OF BARLEY

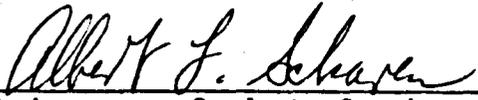
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ABSTRACT

The barley Erysiphe graminis f.sp. hordei host-parasite system was used as a model to evaluate the potential of barley composite cross populations for conservation of disease resistance. The objective was to determine if increases in resistance to powdery mildew could be detected over periods of time in composite cross populations developed in California, where the disease might have had a selective influence on the populations, and the same populations grown in Montana, where no selective influence of powdery mildew was expected. Four isolates of E. graminis f.sp. hordei were used to monitor the frequencies of specific mildew resistances through early, intermediate and late generations of three composite cross populations (CC II, CC V, CC XII) grown at Davis, California, and Bozeman and Moccasin, Montana.

Following artificial inoculation with the powdery mildew cultures in a controlled environment, the barley seedlings were classified as resistant or susceptible according to their reaction types. The number of resistant seedlings was computed for each treatment combination in each replication and converted to a percentage form, on which statistical analyses were performed.

Changes in frequencies of plants resistant to the four isolates were observed between generations in all populations from the three locations. Increases in the frequency of resistant plants were detected by inoculations with culture 59.11 in CC II from Bozeman and CC XII from Bozeman and Moccasin, and by inoculations with cultures 63.12 and MT from the California CC XII. The largest increases in frequency of resistance were detected by inoculations with culture 59.11. CC XII revealed the most and largest increases in resistance of the three barley populations. Trends in the frequencies of resistance are discussed in relation to selection pressure applied by powdery mildew. It is suggested that associations with gene complexes other than resistance to E. graminis might help to explain the increased resistance observed in these studies.

INTRODUCTION

Bulk populations have often been praised as reservoirs of genetic variability, assuring them a wider adaptability under varying and stress environments. Composite cross populations of spring barley (Hordeum vulgare L.) are such "mass reservoirs" containing considerable variability and are suitable both as a means of deriving superior recombinants and for maintaining the variability for further improvements. Barley composite cross (CC) populations, synthesized as early as 1927 have been allowed to reproduce by their natural mating systems in California and Montana, without conscious selection. Evidence for yield improvements, resulting from natural selection of the "fittest" genes and associations, has been shown (25, 29, 65, 77).

Some authors have suggested that plant mixtures might be useful for pest and disease control through host resistance (26, 78). Another improvement in composite cross populations could be the accumulation of genes to obtain higher levels of resistance to pests and diseases. Because composite cross populations are managed so that natural interactions may take place between host and pathogen, it is expected that alleles governing disease resistance will reach frequencies determined by natural selection. But aside from one study on the conservation of scald resistance in barley composite cross populations, this aspect of bulk population use has not been

investigated. In a study of barley scald disease, caused by Rhynchosporium secalis (Oud.) Davis, Jackson et al. (26) found that the frequency of resistant individuals to three of the four isolates of the fungus studied increased significantly in later generations of CC II, whereas little change occurred in the frequency of resistant plants in CC V and CC XII. However, resistance to each isolate was maintained through the latest generations tested of each population.

Erysiphe graminis f.sp. hordei is an obligate parasite and is present all over the world wherever barley is grown. It is highly variable in pathogenicity. The occurrence of powdery mildew is not consistent in the early stages of the barley crop development at Davis, California. Barley powdery mildew is more consistent in the months of January and February and it is then that selective influence from this organism on barley at Davis can be expected (C.W. Schaller, personal communication). In Montana, powdery mildew occurs regularly early in the season. Usually the infection is of short duration and light intensity. Therefore, no selective influence can be expected from the powdery mildew fungus on the CC populations grown at Bozeman and Moccasin, Montana. It was postulated that the frequency of resistant plants would increase from the early to the later generations of the composite, given enough selection pressure exerted by respective races of the pathogen.

The objective of this study was to determine if increase in the frequency of resistant plants to four isolates of powdery mildew could be detected in the populations developed in California as compared to those grown in Montana.

Four isolates of E. graminis f.sp. hordei were used to monitor the frequencies of the corresponding specific resistances in early, intermediate and late generations of three barley composite cross populations grown at three locations.

Variations of resistance to the powdery mildew cultures and conservation of resistant genotypes throughout several generations of each composite cross population are reported in this paper.

LITERATURE REVIEW

The Composite Cross Populations

A survey of recent literature in genetic conservation, phytopathology and crop ecology shows that bulk populations are often praised as reservoirs of genetic variability that assures them wider adaptability under varying or stress environments (41, 77). The term "bulk population" means any population of genotypes that is synthesized by mixing or employing one or more cycles of hybridization and is propagated or used without any artificial selection (29).

A Composite Cross population is such a bulk population, and its use provides one with a breeding method that takes advantage of an initial pool of genetic variability, with natural selection favoring the individuals that are more fit in the competitive sense and/or more fecund, thus evolving toward higher yielding ability (29). Composite cross breeding is also very attractive since a minimum of effort, space and expertise is required (25).

Initial Make-up and Propagation

Through the diligent efforts of H. V. Harlan, G. A. Wiebe, C. A. Suneson, R. W. Allard, E. A. Hockett, and others, we now have in barley a large series of populations originating from composite

crosses involving various schemes of initial hybridization among a diverse set of lines.

The barley populations used for the present studies were three composite cross populations, called Composite Cross II (CC II), Composite Cross V (CC V), and Composite Cross XII (CC XII).

Composite Cross II (C.I. 5461) was synthesized in 1927 by Harlan and Martini from 28 cultivars representing the major barley growing regions of the world (21). The population was created by pooling equal amounts of seed harvested from F1 plants from the 378 possible intercrosses among the parents and it has been propagated in large plots in Davis, California (21, 79, 80), each year under normal agricultural conditions. It was also grown in Montana, but not on a yearly basis.

CC V (C.I. 6620), also developed by Harlan, differs from CC II in both parentage and method of synthesis. The population was developed by pair crossing between 30 cultivars (all six row types) and their progeny to give a single multiple hybrid. The 30 parents, including 11 in common with the parents of CC II, were crossed in all possible pairs, the resulting F1 hybrids again pair crossed, and the cycle repeated until a single grand F1 hybrid was obtained. The population was initiated from selfed seed produced by the grand hybrid in 1941 (79, 80), (Table 1). It has since been propagated in Davis, California, in the same fashion as CC II. It was also

Table 1. History of the initial composition of composite Cross V,
C.I. 6620 (unpublished information, Dr. G. A. Wiebe).

C. I. No.	Cultivar
975	Baker ----- X ^a
1330	Pannier ----- X ^a
4118	Atlas ----- X ^b
1367	Vaughn ----- X ^b
3556	Minia ----- X ^c
1311	Flynn ----- X ^c
6299	New ZZ ----- X ^c
4166	Afghan I ----- X ^d
708	Black Algerian ----- X ^d
2130	Stavropol ----- X ^d
4019	Lioness ----- X ^d
936	Trebi ----- X ^d
6298	Old ZZ ----- X ^d
261	Club Mariout ----- X ^d
6083	Good Will ----- X ^d
6366	Afghan II ----- X ^e
4019	Lioness ----- X ^e
6109	Velvon ----- X ^e
1179	Algerian ----- X ^e
1256	Arequipa ----- X ^e
5888	Rikote ----- X ^e
206	Han River ----- X ^e
14119	Abate ----- X ^e
6265	Ezond ----- X ^e
937	Sandrel ----- X ^e
14061	Bonfarik ----- X ^e
14065	Parla ----- X ^e
3387-8	Maison Carre ----- X ^e
2238	Lion ----- X ^e
6626	Coaston ----- X ^e
5267	Peatland ----- X ^e

a Parents crossed at Aberdeen, Idaho, in 1937

b F₁s crossed at Sacaton, Arizona, 1938

c " " " Aberdeen, Idaho, 1938

d " " " Aberdeen, Idaho, 1939

e " " " Aberdeen, Idaho, 1940

grown in Montana, again, with some irregularity and not always on a yearly basis.

CC XII (C.I. 6705) was developed by G. A. Wiebe and was derived from intercrossing 25 parents. These 25 cultivars, 21 in common with those in CC V and nine in common with those in CC II, were combined through a series of four pairings of F1 plants. In 1940, the residual was backcrossed to the F1 of Atlas x Vaughn (Table 2).

Suneson (77) cited:

"The addition of this final cross is of special interest because of the wide difference in survival ability of Atlas and Vaughn, and the unusual record of an Atlas x Vaughn bulk population which produced four commercially grown varieties Arivat, Beecher, Glacier and Gem."

This population has also been grown in California and Montana.

Population Dynamics: The Composite Crosses

The Composite Crosses of spring barley are not new. They were developed in Davis, California, as early as 1927. The importance of using diverse germplasm in a breeding program and the need to retain variability in the population have been emphasized by many authors (41).

Diversification in populations of predominately autogamous species to provide protection against crop pests was advocated by Suneson (78). CC populations, or "mass reservoirs" containing considerable variability were suitable both as a means of deriving

Table 2. History of initial composition of composite Cross XII,
C.I. 6725 (unpublished information, Dr. G. A. Wiebe)

C.I. No.	Cultivar
4118	Atlas-----X ^a
1367	Vaughn-----X-----
936	Trebi-----X-----
1367	Vaughn-----X-----
1256	Arequipa-----X-----
4019	Lioness-----X-----
4118	Atlas-----X-----
1311	Flynn-----X-----
6298	Old ZZ-----X-----
3387-8	Maison Carree-----X-----
3556	Minia-----X-----
6265	Ezond-----X-----
261	Club Mariout-----X-----
6109	Velvon-----X-----
6298	Old ZZ-----X-----
6251	Olli-----X-----
14065	Parla-----X-----
14119	Abate-----X-----
937	Sandrel-----X-----
5888	Rikote-----X-----
14061	Bonfarik-----X-----
6626	Coaston-----X-----
1111	Chevron-----X-----
1257	Bolivia-----X-----
2238	Lion-----X-----
4166	Afghan I-----X-----
708	Black Algerian-----X-----
6366	Afghan II-----X-----

- ^a Parents crossed at Madison, Wisconsin, in 1937
^b F₁s crossed at Arlington Greenhouse in 1938
^c " " " Madison, Wisconsin, in 1938
^d " " " Arlington Greenhouse in 1939
^e " " " Madison, Wisconsin, in 1939
^f " " " Madison, Wisconsin, in 1940

superior recombinants and for maintaining the variability for further improvement (41). It was suggested that superior recombinants with increased resistance to pests and diseases have been formed and maintained in these populations. Disease control was achieved in these plant mixtures through host resistance. However, in only one study has this important aspect of bulk population use been investigated. Jackson, et al. (26) studied the conservation of scald resistance in three barley CC populations. Four isolates of Rhynchosporium secalis were used to monitor the frequencies of specific scald resistances through early, intermediate and late generations of CC II, CC V, and CC XXI. Resistance to each isolate was maintained through the latest generation tested of each population. Changes in the frequencies of plants resistant to particular isolates were observed between generations in all three populations. In CC II, resistance to three of the four isolates changed from relatively low to extremely high frequencies by the latest generation tested, F47.

Jain and Qualset (29) stated:

"Many epidemiological features of pathogens have been considered in the theories of epidemics. The role of genetic diversity has often been postulated in terms of counteracting such features, but this field is still wide open to critical long-range studies."

So far, only observations of disease resistance in CC populations have been made (25, 29, 78). Bal, et al. (6) looked, among

others, at the characters for scald and net blotch (Pyrenophora teres) resistance in CC II. Suneson (77) studied the impact of a barley yellow dwarf virus infection on CC II in 1951:

"Seven percent of the plants were killed, 38% produced less than 25 seeds per head, and only 27% produced more than 50 seeds per head. This was the first noted impact of this virus on this population, and probably resulted in the greatest differential survival encountered in 25 years."

No critical long-range studies have been conducted on any disease, except scald (26). The same is true for powdery mildew. Its interaction with CC populations has never been thoroughly investigated. Only Hockett, et al. (25) noted about their experiments on CC II: "Apparently the Davis F24 and F35 generations tested in our experiments did not develop disease resistance for powdery mildew or BYDV."

To further understand some of the mechanisms involved in these CC populations, some studies performed on aspects other than accumulation of resistance to pests and diseases will be reviewed. These aspects may reveal certain patterns of response within the populations, which, in turn, may explain the response of these host populations to selection pressures from diseases. Jain (27) stated:

"The key issues raised at population level often relate to the analyses of form and amount of genetic variability, the mode and intensity of selection pressures, role of heterozygosity in the performance and evolutionary flexibility, adjustments in the genetic system, and the relationship between certain measures of productivity and stability."

The following topics are discussed: 1) Yield and adaptation studies, 2) Possible uses of the CC populations, and 3) Specific studies performed on the three CC populations used in this study.

Yield and adaptation are discussed because these factors showed how selective forces were acting upon CC populations, and how the populations were reacting to them. Adaptation also explains population stability.

Uses of CC populations are also presented because this topic raises questions on future population management schemes. The methods used to work the CC populations are largely dependent upon the results one wishes to obtain from the populations.

Not many aspects of population use for disease control have been investigated. More comparative studies need to be done for a better understanding of the genetics involved in population breeding.

Yield and Adaptation Studies

Studies on bulk yields of four CC populations of barley (CC II, V, XII, and XIV) were done by Suneson (77) and showed that the initial yield of each of the original CC populations was lower than that of the same check cultivar Atlas 46. Yields remained unchanged up to F6, after which they were improved, and surpassed the yield of the check by F20. Suneson also presented data from the yield

performance of random selections from different generations of CC II. None of the F2 selections from CC II exceeded the yield of Atlas 46, but of 50 F20 selections one outyielded Atlas 46 by an average of 37%. The three top selections from F24 gave an average of 56% yield increase over the check. However, from the F2 to F40 approximately a 50% yield gain resulted from natural selection of the "fittest" genes and associations (79). Hockett, et al. (25), however, did not find such large increases in their trials with CC II in the disease and high yield environment at Davis, California.

While Suneson's (77) results showed that populations did not improve until the F7 generation, Rasmusson, et al. (65) observed a rapid improvement in yield over six years in a composite population obtained by mixing seed from 6,000 entries in the world collection. The difference may lie in the numbers of initial cultivars or parents and superiority of the base population. The presence of many inferior segregates in the early generations may slow down initial improvement (41).

Harlan and Martini (21) found that the less adapted cultivars were rapidly eliminated in a specific environment. Under natural selection, genotypes with specific adaptations were at a disadvantage and were gradually eliminated from the population. Widely adapted genotypes were favored (41).

Jain and Qualset (29) also studied the population structure and evolutionary dynamics of several composite crosses. By scoring the genotypic frequencies at several marker loci during successive generations, a variety of selective changes that occurred during many years of cultivation were shown. They stressed the importance of the number of macro- and micro-environments to be used in either the propagation or evaluation of the CC populations, since the adaptive role of genetic variation is the central issue. Hockett, et al. (25) also emphasized this point in their study on CC II in three different environments.

Uses of Composite Cross Populations

One of the attractive aspects of CC breeding is that benefits are expected, through low cost maintenance of populations, from the interplay of recombination and natural selection. Recombination ensures the appearance of new genotypes in the first few generations of bulk propagation. In the absence of any mechanism for prolonging heterozygosity, the majority of genotypes in such a population is expected to be homozygous by about F6 (30). Hockett, et al. said that new gene combinations would be fixed by F8 (25). Suneson (77) then suggested that 15 generations of natural selection seem desirable. Thereafter, there can be repeated recourse to three breeding

methods: 1) Continued natural selection with prospects for significant gains in yield to accrue throughout a working lifetime. However, Lohani (41) reported that there is a limit beyond which CC populations might not improve for yield, depending greatly on the characteristics of the base population. 2) The use of cyclic hybrid recombinations with intervening natural selection to give a kind of recurrent selection. An example is the work currently in progress at MSU with recurrent selection populations of barley containing broad based resistance to several diseases. The use of male sterility in various ways offers a very useful tool for regulating the breeding structure of a population. 3) The use of conventional selection and testing. Some authors (29, 30, 39, 41) strongly advocate the use of selection and exploitation of the populations to overcome the very serious losses of desirable genes which have been observed in populations due to selective disadvantage. Tee and Qualset (29) proposed a population-management scheme in deriving pure line cultivars, based on the single-seed descent methods for maintaining variability. This method minimizes natural selection but still allows the breeding system to be varied for influencing population changes.

Other modifications to be adopted in a breeding program were suggested by Khalifa and Qualset (39), such as the use of wider

spacing to decrease the effect of competition, and early (F2) subdivision of the population into separate groups based on the characters known to be important in competition.

As Allard mentioned (personal communication) a CC population as a whole is a stable system, with a fantastic amount of genetic variability. The population in and of itself is not a breeding method, but rather a good way of conserving variability, and a good source of plant materials.

Many authors agree (25, 29, 30, 39) that CC population development should be an integral component of any breeding program, but only as a complement to other breeding methodologies which are more time efficient (25) than those associated with CC populations.

Jana, et al. (30) stated:

". . . the bulk-population breeding method is too slow despite its attraction in view of the economy of management and the danger of over indulgence in pure-line breeding."

Thus, a wise combination with other breeding methods may be more appropriate.

Some important considerations concerning each CC population, such as its initial synthesis, its fitness versus agricultural productivity relative to a theory of evolution, determine the methodology applied to a given population. Each of these considerations raises a series of questions, such as (29):

"Is the performance of mixtures dependent on the number of lines and their relative proportions? Do gene interactions play an important role in selective changes, and, if so, are certain optimal levels of recombination needed to generate and then preserve linked gene complexes? How often do disease and pest occurrences show genetic diversity to be highly desirable?"

A scientific answer to any one of the issues raised depends on the accumulation of statistical tests on many comparable studies appropriately designed.

Some Specific Studies Performed on the Three Populations

CC II. CC II was the principal gene pool used for a thorough study on breeding methods by its originators (29). They used it to develop an evolutionary breeding method (77); to make studies on population dynamics (6); and to point to genetic diversity as a mechanism for control of diseases and insects (78). The Montana Agricultural Experiment Station has the same gene pool grown independently (79). Hockett, et al. (25) have used the composite cross II, developed by natural selection under three different environments (one in California and two in Montana) and tested in these and other diverse environments, to evaluate agronomic improvement and stability over several years. CC II, together with CC V, was also used in a study on biochemical properties of polymorphic esterases by Edwards (16), and by Allard, et al. (3, 37). Clegg, et al. (13) studied the dynamics of gametic frequency change in CC

II and CC V. Jackson, et al. (26) have used CC II and CC V in a study of the conservation of scald resistance. Since evidence was shown for correlations between different genetic loci in highly self-pollinating populations such as CC populations (13, 84), Muona, et al. (62) investigated possible correlations between the observed changes in resistance in CC II to different isolates of scald, the same as used by Jackson, et al. (26).

CC V. Even though 15 generations behind CC II, evolutionary developments have complemented the more advanced population and confirmed that striking yield improvements accrue over time (79). CC V was the principal barley resource material used by Allard and Jain in their studies of population dynamics (2, 28). Also, Lohani (41) described the results of his investigations in South Australia on the yield and adaptation of selections from various generations of CC V and their association with some physiological and agronomic characters. Studies on allozyme polymorphisms (84), mating system (38), and components of selection (14) in an experimental plant population, were also performed on CC V.

CC XII. CC XII was not used intensively in experimental studies. It closely resembles CC V, with the exception of a final backcross to the F1 of Atlas and Vaughn (Table 2). Suneson (79) ascribed the lack of studies on CC XII to a presence of fewer conventional marker genes. The California CC XII F26 embodies more

heterozygosity and other positive characters, and is more productive than the California CC II F40 and CC V F25 (77).

The Fungus

The Disease Organism

Powdery mildew fungi are obligate parasites which infect a wide range of host plants throughout the world. The extensive literature on powdery mildew of cereals and various grasses caused by the fungus Erysiphe graminis DC., indicates that this organism is of considerable economic importance in many parts of the world. In Europe, it is one of the main diseases causing enormous losses. Powdery mildew, with scald and barley stripe, are the most destructive diseases of barley in California (69). While not as spectacular as barley stripe or such diseases as stem rust (Puccinia graminis f.sp. tritici) and bunt (Tilletia spp.) of wheat, the widespread distribution and annual occurrence of powdery mildews make them a potential threat to barley production.

The classification of the powdery mildews is as follows:

Class: Ascomycotina
 Subclass: Eusacomyces (asci are produced in an ascocarp)
 Series: Plectomyces (having a closed ascocarp or cleistothecium)
 Order: Erysiphales (obligate parasites)
 Family: Erysiphaceae (mycelium on the surface of the host plant)
 Genera: The genera are distinguished from each other by the number of asci they produce per cleistothecium, by the morphology of hyphal appendages growing out of the wall of those cleistothecia, and by host specialization.

The genus *Erysiphe* has more than one ascus per cleistothecium. The complete name of powdery mildew on barley is *Erysiphe graminis* DC. f.sp. *hordei* Em. Marchal (51).

Barley powdery mildew is an obligate parasite with superficial growth. It never invades the tissues of the host, but sends out specialized structures, haustoria (7), into the epidermal layer for feeding purposes. Its mycelium is heterothallic: an antheridium and ascogonium form the cleistothecium, which represents the overwintering or oversummering form.

The powdery mildew fungi, although they are common and cause serious diseases in humid areas, are even more common and severe in warm, dry climates because their spores can be released, germinate and cause infection at any relative humidity level in the air without need for the presence of a film of water on the plant surface (free moisture) (83). Once infection has begun, the mycelium continues to spread regardless of the moisture conditions in the atmosphere.

Life Cycle

The life cycle of *Erysiphe graminis* f.sp. *hordei* consists of:

- 1) a sexual stage and 2) an asexual stage.

The Sexual Stage

Cleistothecia produce asci, in which ascospores are formed. Cleistothecia, the survival structures, were produced by a heterothallic mycelium. The cleistothecia remain viable for a very long period of time (56). In a suitable environment (12, 20), cleistothecia crack open by a swelling of the contents (83). The asci are then thrown out and they discharge their ascospores. Usually eight ascospores are produced in each ascus. Ascospores are able to infect green living tissue immediately, but they can also survive some harsh environmental conditions and still be infective.

The Asexual Stage

The imperfect stage is characterized by the formation of conidia. The conidia of E. graminis f.sp. hordei belong to the form genus Oidium of the Fungi Imperfecti. The conidia are much more sensitive to environmental conditions than the ascospores. They cause secondary infections and are responsible for the spread of the disease (83).

Environment and Infection Process

Many investigations have been conducted upon the effects of temperature, relative humidity and light on the germination of powdery mildew conidia (12, 17, 18, 42, 54). Much emphasis has been placed on the effects of various environmental factors on the

progress of disease development, in order to characterize and define the events of the primary infection process and the genetic regulation of the events which occur during initial host-parasite interactions. Initially researchers (1, 10, 20, 44) studied environment and the biological systems on a quantitative basis. A quantitative approach reduced the variability in the results obtained, thereby improving the understanding of the establishment of a parasitic relationship (18, 21).

The sequential development of powdery mildew on the plant surface is divided into nine stages (61):

1. germination of conidia
2. production of "club-shaped" appressorial initials
3. maturation of appressoria
4. penetration of the cuticle and epidermal cells
5. formation of haustoria
6. formation of secondary hyphal initials
7. elongation of secondary hyphae (ESH)
8. initiation of additional infections, and
9. sporulation.

Each of these development stages differs in its requirement for, and sensitivity to, temperature, relative humidity and light (63, 64). When the optimum conditions for each stage are present, a high percentage of the parasite population undergoes these various development stages with increased synchrony at each stage, and a high infection frequency is obtained. High infection frequency means that a high percentage of conidia, placed on a plant surface, were able to form elongating secondary hyphae and show a compatible

relationship. The elongating secondary hyphae (ESH) are generally used as a criterion for the establishment of a functional, compatible host-parasite relationship, since only those parasitic units which form functional haustoria can form ESH (43).

Genetics of the Host-Parasite Relationship

In an incompatible relationship, genes for resistance in the host can affect powdery mildew strains differently: haustoria may not develop, or no ESH will form. An historical breakthrough came with Flor's gene-for-gene concept (29) and the quadratic check, as a general rule for many host-parasite relationships (18) (Figure 1).

Only in combining the two organisms and by examining the reaction type of the host as it responds to the infection of the pathogen is identification of either the host or the pathogen possible. An incompatible relationship is one in which a resistant host genotype interacts with the corresponding avirulent type of the pathogen. An advantage of this abbreviated graphic explanation is that neither ploidy nor heterozygosity alter the generalization that only corresponding P/R genotypes act to restrict disease development and do so regardless of the other corresponding gene pairs in the host-parasite genotypes (Figure 1).

The barley powdery mildew terminology, proposed by Loegering and used by Moseman (53), is used in this investigation (Figure 2).

		PARASITE	
		P	p
HOST	R	-	+
	r	+	+

Figure 1. Host-parasite relationship in a quadratic check. Genes conditioning resistance (R) and avirulence (P) are dominant. Genes for susceptibility (r) and for virulence (p) are recessive. (+) = compatible relationship; (-) incompatible relationship. From Ellingboe (18)

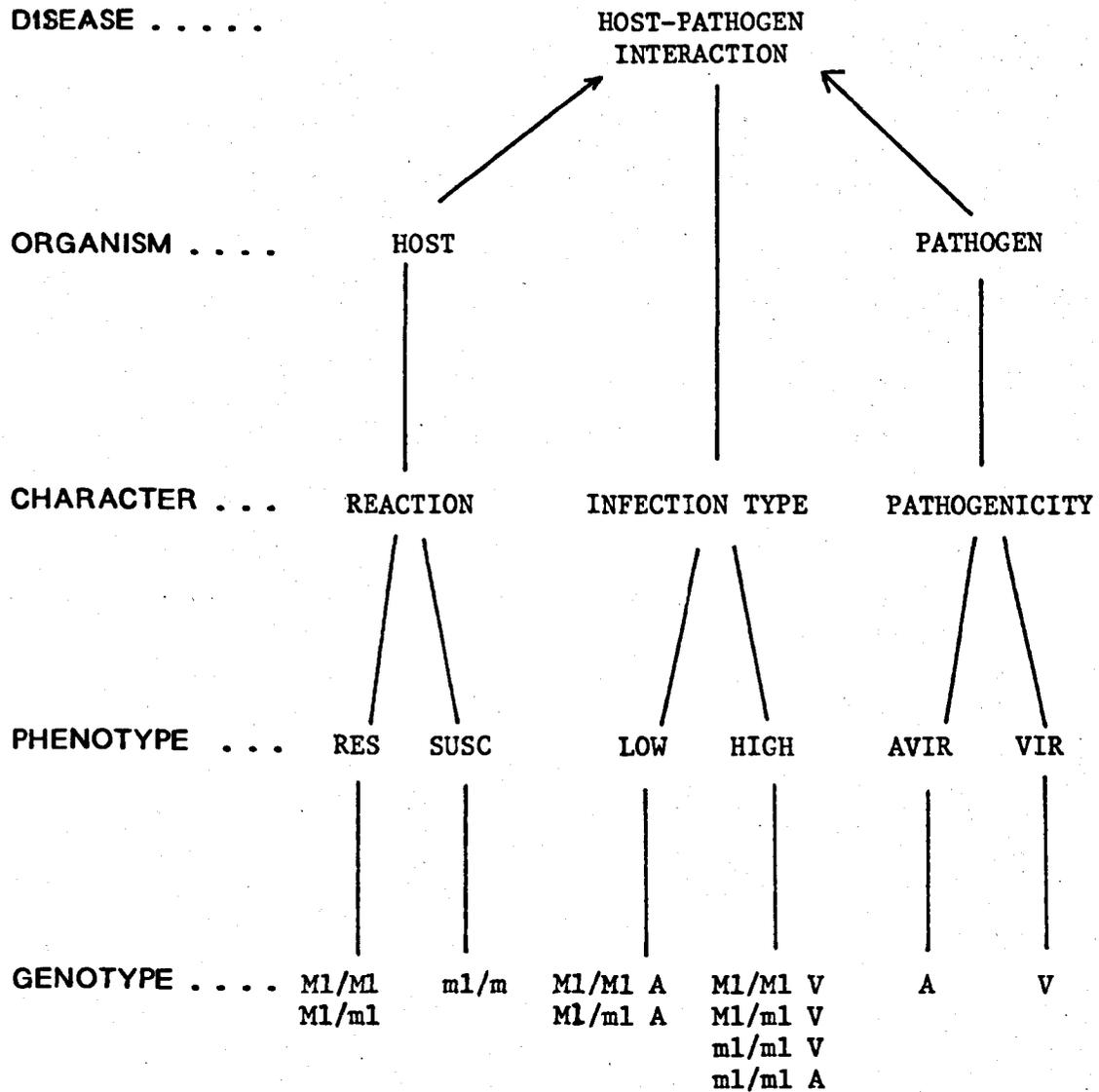


Figure 2. Diagram of how gene interactions between host (barley) and pathogen (*Erysiphe graminis* f.sp. *hordei*) result in the disease (barley powdery mildew). From Moseman, 1971 (53).

Genes

Some 40 genes for resistance to Erysiphe graminis f.sp. hordei are known in barley. Table 3 represents some well known and characterized resistance sources and genes in barley to powdery mildew (24). The significance and origin of the host gene symbols in Table 3 is as follows (52): 1) The letters Ml refer to genes conditioning the reaction of varieties to Erysiphe graminis f.sp. hordei (The abbreviation Ml indicates a gene in the dominant condition, and ml indicates a gene in the recessive condition.); 2) The letters and superscripts following the letters Ml refer to specific genes; and 3) the letters identify the locus and the superscripts number the specific gene at that locus.

Most of those genes are located on chromosome five of barley. Only the ml-o and Ml-g genes were found to be on chromosome four (35, 36, 51, 69, 70). The ml-o gene is also the only recessive gene known for powdery mildew in barley. For the 40 known genes, at least seven loci are recognized with at least 17 distinct alleles conditioning resistance (86).

Linkage Maps of Barley

All the known genes for resistance to powdery mildew are located on chromosomes four and five of barley. The linkage maps in barley by Tsuchiya (81, Appendix 1) show three genes for powdery

Table 3. Sources of resistance against Erysiphe graminis in barley.
See text for explanation of the host gene symbols.

Genes for Resistance	Variety Adapted from Hermansen (24)	Variety Adapted from other sources (51,52,85)
M1-a	Iso 1 R C.I.16137	Rabat C.I.4979 (50,53)
M1-a2	Black Russian C.I.2202	(50)
M1-a3	Ricardo C.I.6306	(50)
M1-a4	No 22 C.I.13654	(55)
M1-a5, M1-a? ^a	Gopal C.I.1091	(55)
M1-a6	Voldagsen 8141/44	1-Gatersleben Mut.501 C.I.13132 2-Hordeum spontaneum nigrum C.I.13130(51)
M1-a7, M1-a?	Visir	/ ^b
M1-a8	Heil's Hanna C.I.682	/
M1-a9, M1-a4	Mona	/
M1-a10	Iso 12 R C.I.16149	/
M1-a11	A222 C.I.11555	/
M1-at	Atlas C.I.4118	(50,53)
M1-a, M1-at	Algerian C.I.1179	(50)
M1-a?	/	1-Cebada Capa C.I.6193 2-Multan C.I.3401
M1-c	Indian HOR 1657	/
M1-g	Iso 2 R C.I.16139	Goldfoil C.I.928 (50,60)
M1-a?, M1-g	/	Palmella Blue C.I.3609
M1-h	Weihenstephan 37/136	1-Wehenstephan St. 37/136 2-Chevron C.I.1111(60)
M1-k	Iso 4 R C.I.16143	Kwan C.I.1016 (50)
M1-n	Gatersleben Mut.411 C.I. 13131	1-Gatersleben Mut. 511 C.I. 13131 2-Nepal C.I.595 (50)
m1-05	Risø 5678 C.I.15219	/
M1-(La)	Lofa Abed	/
M1-(GM501), M1-?	Gatersleben Mut.501 C.I.13132	/
M1-p	Iso 5 R C.I.16145	Psaknon
?	/	Lyallpur BS C.I.3395
?	/	Lyallpur C.I.3403

^a? = unknown location of the resistance gene on the barley chromosome.

^b/ = not applicable.

mildew resistance in the short arm of chromosome five: Reg 1, Reg 4 and Reg 5 (Reg = resistance to E. graminis is the new notation for powdery mildew resistance genes on the chromosome maps).

Tsuchiya (81) also mentioned some other genes for powdery mildew resistance associated with chromosome five: Ml-at, ml-d and Ml-nn. Following the linkage map of chromosome five by Jensen (32, Appendix II), all the known genes for resistance to powdery mildew on chromosome five are located on its short arm: Ml-at, Ml-a (= Reg 1), Ml-k (= Reg 4), ml-d, Ml-nn and Ml-p (= Reg 5). Therefore, the probability of close connection or linkage is great between these resistance genes for powdery mildew and the following genes and/or loci:

- 1 - Pa 4 = Rph 4, resistance to Puccinia hordei;
- 2 - Hor 1, Hor 2, Hrd C, Hrd D, Hrd E, the hordein series;
- 3 - Yr 4 = Rps 4, resistance to P. striiformis;
- 4 - Lys 4d, high lysine.

Jensen, et al. (33) studied the linkage of the hordein loci with the powdery mildew resistance loci on chromosome 5. The recombination percentage between Ml-k and Hor 1 was estimated to be $4.0 + 1.3$, between Hor 1 and Ml-a, $5.3 + 1.1$, and between Ml-a and Hor 2, $6.1 + 1.2$. This association renders the hordein loci very useful as marker genes (15). The other genes on the short arm of

chromosome five were not cited in the literature of the CC populations.

Bal, et al. (6) studied some character associations in CC II. Heading date, spike density and waxy characteristics were regulated by genes on the long arm of chromosome five. Suneson and Stevens (80) described the rapid decline of the black seed character (B-series on the long arm) in CC II after about 12-15 generations. Jain and Qualset (29) summarized the evidence on the nature of the selective forces in CC populations (Appendix III). However, no indications of linkage were found between these potential markers and any known genes on chromosome five.

Two genes for powdery mildew resistance are located on the short arm of chromosome four: Reg 6 (= ml-o) and Reg 2 (= Ml-g) (Appendix I). Other genes resident on the short arm of chromosome four which might form associations with powdery mildew resistance genes have been investigated. Bal, et al. (6) studied character association with plant height (min and br) and waxy character (cer). Haus (23) found a recombination percentage of about 5% between the brachytic 2 (br 2) gene and Ml-g. Suneson and Stevens (80) described the decrease of the hooded character (K-series) in CC II from the F4 to the F23. The K-series, however, are located on the long arm of chromosome four (Appendix I) and possible linkages with genes for resistance to powdery mildew are unlikely.

Tsuchiya (81) and Haus (23) also included lists of genes associated with chromosome four. The male sterile gene (msg 24v, msg 25r) and the bl- gene for aleurone color may show some association with ml-o and Ml-g. Harlan and Martini (22) found this aleurone color not to be related to yield. Jain and Qualset (29) summarized the evidence on the nature of selective forces in CC populations of barley (Appendix III).

Genetic Action

The genes for resistance do not appear to operate by inhibiting the initiation of penetration of the host by the appressoria of the parasite. On susceptible and resistant cultivars, spores or conidia can land on the plant surface, germinate and make a close contact between appressorium and cuticle. This is followed by the early appearance of a deposit adjacent to the inner surface of the epidermal wall below the point of contact. Since these deposits are similar in resistant and susceptible cultivars, apparently they are not the prime mechanism of resistance (75).

The resistance seems to depend on hypersensitive responses. Different responses are obtained in function of the genes for resistance present, and are sometimes initiated before the pathogen has entered the lumen of the cell (11). Ellingboe (17, 18) has proposed that contact between the pathogen and plasmalemma of the

host is necessary for a resistant response. Genes for resistance can stop the development of the pathogen upon contact with the host plasmamembrane. For example, in the presence of the Algerian gene, Ml-a, 95% of the parasitic units do not produce haustoria, as opposed to a compatible relationship, in which 90% of the spores will produce haustoria (17).

Masri and Ellingboe (43) describe some resistant reactions for the following genes: 1) the Ml-a gene causes distortion of haustoria; 2) the Ml-g gene inhibits secondary infection; 3) the Ml-k gene causes collapse of host tissue; and 4) the Ml-p gene inhibits growth and sporulation. All these genes have different effects on the fungus at different stages of the fungal development. Other known genes for resistance to powdery mildew and their inheritance are described by several authors (8, 47, 48, 58, 59, 61).

For its survival, this obligate parasite must not kill the host cell. Compatibility or incompatibility can occur at any stage of infection by alteration in any one of the large number of physiological systems during the infection process. In fact, an infinite number of different mechanisms could be involved in incompatibility responses (9, 70).

Effect of Powdery Mildew on
Barley

In an analysis of the effects caused by powdery mildew on barley, the following factors will be considered: 1) first appearance of the powdery mildew on the barley; 2) growth stage at which the barley crop is attacked; and 3) duration and severity of the infection.

Infection by powdery mildew results in gradual decline in vigor and growth. First, increased respiration is observed on infected plants, with a respiratory rate well above that of healthy plants of the same age. Reported oxygen consumption was from 250 to 650% more than with healthy plants (5, 67). This increased respiration eventually leads to the depletion of the carbohydrate reserves of the host, which can cause the vegetative growth of the fungus to slow down (4).

Smedegaard-Petersen (72) observed increased respiratory activity in highly resistant host-pathogen combinations with an incompatible relationship, where the host showed a hypersensitive reaction. This incompatibility is associated with a number of biochemical and structural defense reactions. These require energetic and biosynthetic activities which may deprive the host of energy and ultimately lead to a lower yield (72).

Smedegaard-Petersen and Stolen (74) studied the effect of these energy requiring defense reactions on the yield and grain quality in a powdery mildew resistant barley cultivar. Grain yield was significantly reduced by seven percent and the kernel weight by four percent. There was a reduction of 11% in the yield of the grain protein.

Smedegaard-Petersen and Stolen (73) also presented an overview of the known changes in biochemical activity in incompatible combinations between barley and the powdery mildew fungus.

Schaller (68) studied the effects of powdery mildew on barley yield and its components: a) number of tillers per plant; b) number of kernels per spike; and c) kernel weight.

The cultivar Atlas and its isogenic Atlas 46, which was resistant to the powdery mildew cultures occurring in California, were planted in paired plots at several locations throughout California over a three-year period. No attempt was made to control or initiate disease development. In all three years, powdery mildew infection was widespread during the early stages of the barley development, causing considerable yellowing and defoliation of the young plants. Only in one out of the three years did late spring rains favor continuous development of the powdery mildew up to and including infection of the flag leaf. Symptoms then were abundant sporulation and leaf-yellowing. Under disease-free conditions no

difference was found in the yield of Atlas and Atlas 46. Powdery mildew infection of light intensity and short duration, present only in the early phases of the plant development in two out of the three years, reduced the yield of Atlas by 6.6 and 3.8%, and the number of kernel per spike by 14.9 and 8%, respectively. The average losses for the three years under heavy infection were 17.6, 14.0 and 8.1% of the total yield. The maximum reduction at any one location was 27% of the total yield. Continuous infection throughout the growing season resulted in an average reduction in kernel weight of 6.4% and in kernel number of 21.5%. Schaller (68) stated:

"One of the most significant findings of this study was the measurable effect of limited infection occurring early in the season. Infection of the above intensity and duration is normally overlooked or ignored, and, since the plants fully recover and produce kernels of average weight, the resultant damage is not evident at harvest."

The effects of powdery mildew on the yield and yield components of several barley cultivars were studied by Scott, et al. (71) in a controlled environment. Pot-grown barley plants were exposed to infection by powdery mildew at different growth stages and for different periods of time. Powdery mildew infection was assessed in terms of percentage leaf area covered and at harvest the kernel weight per plant, kernel size and tiller number were recorded. Powdery mildew attacks up to growth stage (G.S.) 5.0 of the Feekes scale (40) reduced the number of fertile tiller up to

30% at harvest. These early mildew attacks also reduced the number of kernels per spike up to 11%, even when the disease was controlled during later stages of growth. Powdery mildew infection after G.S. 5% reduced mainly the kernel weight and the number of kernels per spike. At these later stages, losses were in the order of 6% in kernel weight and 13% in number of kernels per spike.

Johansen (34) reported the results of his four-year long experiments on spring barley varieties in Denmark. His barley plots were artificially inoculated with mildew after G.S. 5.0. He found an average yield loss due to mildew of 15.7%, varying from 10 to 22.5%.

Yield losses are largely dependent on the stage of plant development at which powdery mildew infection is initiated and on the subsequent duration and severity of infection. Studies on the physiology and development of the barley plant help explain these effects of early powdery mildew infection on the number of tillers per plant and the number of kernels per spike. Tillers and kernels primordia in barley are produced at an early stage, before G.S. 5.0. Infection during these phases of plant growth will then have deleterious effects on both the tiller and kernel primordia (71). Late powdery mildew attack reduces the kernel weight and this is normally explained as resulting from reduction in photosynthate at grain filling.

MATERIALS AND METHODS

The Composite Cross Populations

Random seed samples from early, intermediate and late generations of each CC population were obtained in 1979 from Dr. R. W. Allard of the University of California, Davis, and from Dr. E. A. Hockett of U.S.D.A. and Montana State University.

Since a minimum of 100 seedlings was needed for testing and reading one replication of each generation, the percentage germination of each seed sample was calculated. The number of replications needed for each generation was then adjusted accordingly so that about 300 readings were obtained for one generation-testing by each isolate of the powdery mildew fungus.

Seed from the following generations of each CC population from California and Montana was used in these experiments. The selection of early, intermediate and late generations of each CC population was made on the basis of even distribution between the generations as well as seed availability.

California

CC II (C.I. 5461) (Table 4). This population was grown at Davis, California on a yearly basis since its synthesis in 1927.

Table 4. History of composite Cross II grown at three locations from its synthesis to 1980.

Year	California		Montana		Year	California		Montana	
	Davis		Moccasin	Bozeman		Davis		Moccasin	Bozeman
1927	F1				1954	F28	F16	F29	
1928	F2				1955	F29	F17	F30	
1929	F3				1956	F30	F18	F31*	
1930	F4	(F3)			1957	F31	F19	F32	
1931	F5	(F4)			1958	F32	F20*	F33	
1932	F6	(F5)			1959	F33	F21	F34	
1933	F7	(F6)			1960	F34	F22	F35	
1934	F8*	(F7)			1961	F35	F23	F36	
1935	F9	(F8)			1962	F36	F24	F37*	
1936	F10	(F9)			1963	F37	F25*		
1937	F11	(F10)			1964	F38			
1938	F12	(F11)			1965	F39			
1939	F13				1966	F40			
1940	F14				1967	F41			
1941	F15				1968	F42			
1942	F16*				1969	F43			
1943	F17	(F12)			1970	F44			
1944	F18	F13*			1971	F45			
1945	F19				1972	F46			
1946	F20				1973	F47			
1947	F21				1974	F48*			
1948	F22				1975	F49			
1949	F23				1976	F50			
1950	F24			(F25)	1977	F51*			
1951	F25			F26*	1978	F52			
1952	F26*	F14		F27	1979	F53			
1953	F27	F15		F28	1980	F54			

*Generations tested in this study.

Seed of the following five generations was obtained: F 8-16-26-48 and 51. These five generations tested represented a period of 43 consecutive growing seasons. Only in the F8 generation was the germination percentage low (79%).

CC V (C.I. 6620) (Table 5). CC V was also grown continuously at Davis, California since its synthesis in 1941. The F6-13-24-33 and 36 generations of this population were tested. These five generations represent a period of 30 consecutive years. All the seed samples contained healthy seed with a germination percentage of 90% and more.

CC XII (C.I. 6725) (Table 6). CC XII was grown on a yearly basis at Davis, California since it was originated in 1940. The F6-16-24-29 and 35 generations were tested from this population in this study. These five generations cover a period of 29 consecutive years. Generations 6, 16, and 24 had the average germination of 76%, 75% and 70%, respectively.

Montana

Moccasin Populations

CC II (C.I. 5461) (Table 4). From this population seed was available from the F13 to F25. The F13 was grown in 1944 and had a germination percentage of about 92-93%. F20 was chosen as a representative of an intermediate generation and F25 of a later one.

Table 5. History of composite cross V grown at three locations, from its synthesis to 1980.

Year	California		Montana		Year	California		Montana	
	Davis		Moccasin	Bozeman		Davis		Moccasin	Bozeman
1941	F1				1961	F21	F15		
1942	F2				1962	F22	F16		F10
1943	F3			(F3)	1963	F23	F17		F11
1944	F4	F4		(F4)	1964	F24*	F18		F12
1945	F5	F5		F5*	1965	F25	F19		F13
1946	F6*			F6	1966	F26			
1947	F7				1967	F27	F20*		
1948	F8				1968	F28			
1949	F9				1969	F29			
1950	F10				1970	F30			
1951	F11				1971	F31			
1952	F12	F6			1972	F32			
1953	F13*	F7			1973	F33*			
1954	F14	F8			1974	F34			
1955	F15	F9			1975	F35			
1956	F16	F10			1976	F36*			
1957	F17	F11	F7		1977	F37			
1958	F18	F12*	F8		1978	F38			
1959	F19	F13	F9*		1979	F39			F14*
1960	F20	F14			1980	F40			

*Generations tested in this study.

Table 6. History of CC XII grown at three locations, from its synthesis to 1980.

Year	California		Montana		Year	California		Montana	
	Davis		Moccasin	Bozeman		Davis	Moccasin	Bozeman	
1940	F1				1961	F22			
1941	F2				1962	F23	F16		F11
1942	F3		(F3)	(F3)	1963	F24*	F17		F12
1943	F4		(F4)	(F4)	1964	F25	F18		F13
1944	F5		(F5)	(F5)	1965	F26	F19		
1945	F6*		F6*	(F6)	1966	F27			
1946	F7			F7*	1967	F28	F20*		
1947	F8				1968	F29*			
1948	F9				1969	F30			
1949	F10				1970	F31			
1950	F11				1971	F32			
1951	F12				1972	F33			
1952	F13		F7		1973	F34			
1953	F14		F8		1974	F35*			
1954	F15		F9		1975	F36			
1955	F16*		F10		1976	F37			
1956	F17		F11		1977	F38			
1957	F18		F12	F8	1978	F39			
1958	F19		F13	F9*	1979	F40			F14*
1959	F20		F14	F10	1980	F41			
1960	F21								

*Generations tested in this study.

CC V (C.I. 6620) (Table 5). Seed from the F4 to F20 was available. Unfortunately, seed samples from F4, F5 and F6 did not germinate at all. Samples from the F7 had a very low germination of 10%. For the isolate-testing, the F12, grown in 1958 and the F20, grown in 1967 were used.

CC XII (C.I. 6725) (Table 6). Generations F6 and F20 were tested. The F11 and F12 were also included in the tests, but did not germinate. The F6 was grown in 1945 and F20 in 1967.

Bozeman Populations

CC V and CC XII were grown and maintained in Bozeman. CC II, however, was grown in California for 24 generations and from the F25 on, in 1950, in Bozeman.

CC II (C.I. 5461) (Table 4). The F1 to the F24 were grown at Davis, California, from 1926 to 1950. In 1950, the seed from F24 was received in Bozeman and immediately planted to form the F25 the same year. The F25 seed for these tests did not germinate. The F26, F31, and F37 were tested. The F26 had germination of only 55%.

CC V (C.I. 6620) (Table 5). Seed was available from the F5 and F14. The F5 was grown in 1945 and germinated very well. The F9 was grown in 1959 and the F14 in 1979, and these two generations also germinated well.

CC XII (C.I. 6725) (Table 6). The F7 to the F14 were available from this population. Generation F7 had a germination of only 30-40%.

Table 7 shows the number of seedlings tested and the number of replications used for each generation of each composite to the four isolates of powdery mildew.

Seed of the parents of each CC population was obtained from the Small Grains Collection of the U.S.D.A. Agricultural Research Service of Beltsville, Maryland.

The CC populations were grown in large plots in California and in Montana, without conscious selection. Each population was exposed to disease pressure which varied from year to year with environmental conditions and a variable E. graminis f.sp. hordei population.

The weather conditions were conducive to the development of the fungus each year during the growth season of the barley crop in California where barley is grown from November to April-May.

Schaller noted (personal communication):

"The occurrence of powdery mildew at Davis is not consistent in the early stages of the barley crop development. Suneson used to plant the CC populations early, in November or December. Barley powdery mildew is more consistent in the months of January and February. It is then that selective influence from the powdery mildew organism on the composite cross populations at Davis can be expected."

Table 7. Total number of seedlings evaluated in three replications for each generation-isolate combination of three CC populations at three locations.

CC	Location	Generation	Isolate of <i>E. graminis</i> f.sp. <i>hordei</i>			
			MT	59.11	63.12	64.54
II	CAL ^a	F 8	250	235	224	158
		F 16	304	309	318	318
		F 26	300	313	316	317
		F 48	304	289	323	338
		F 51	312	313	312	370
II	MOC ^a	F 13	300	305	328	322
		F 20	304	305	335	343
		F 25	305	295	326	345
II	BOZ ^a	F 26	169	159	226	337
		F 31	303	300	204 ^b	324
		F 37	311	287	335	347
V	CAL	F 6	286	279	321	337
		F 13	283	291	328	343
		F 24	293	294	308	348
		F 33	308	283	307	320
		F 36	321	305	442 ^c	353
V	MOC	F 12	302	294	338	339
		F 20	289	291	219	352
V	BOZ	F 5	294	397 ^c	315	332
		F 9	304	287	325	327
		F 14	327	303	341	342
XII	CAL	F 6	244	249	310	373
		F 16	212	236	262	412 ^c
		F 24	204	213	229	280 ^c
		F 29	309	294	391	397
		F 35	307	293	350	360
XII	MOC	F 6	306	308	325	346
		F 20	298	276	349	314
XII	BOZ	F 7	84	97	124	234 ^c
		F 9	289	272	332	327
		F14	328	327	349	361

^aCAL = California; MOC = Moccasin, MT; BOZ = Bozeman, MT.

^bTwo replications.

^cFour replications.

Schaller also mentioned (68):

"Powdery mildew, Erysiphe graminis hordei Marchal, and Rhynchosporium secalis (Oud.) Davis, rank with barley stripe as being the most destructive diseases of barley in California. While not as spectacular as barley stripe or such diseases as stem rust and bunt of wheat, their widespread distribution and annual occurrence make them a potential threat to barley production year in and year out."

In Montana barley is grown from April 20-30 to around August 15 in Moccasin, and from April 25-May 5 to about August 20 in Bozeman. Powdery mildew has been observed regularly early in the season in Bozeman, Montana and in the irrigated fields in the Fairfield area (personnal communication, Drs. Scharen and Sharp). Symptoms include sporulating lesions, yellowing and loss of lower leaves. The symptoms usually do not progress beyond the lower leaves.

Environment for the Experimental Study

Two environmental growth chambers were used. The area of growing space for the seedlings was 51 x 65 x 118 cm. These chambers were kept at a standard environment throughout the experimental research (12, 17).

Light Conditions

Twelve hours of darkness alternating with 12 hours of light were used. The illumination was provided by six fluorescent tubes

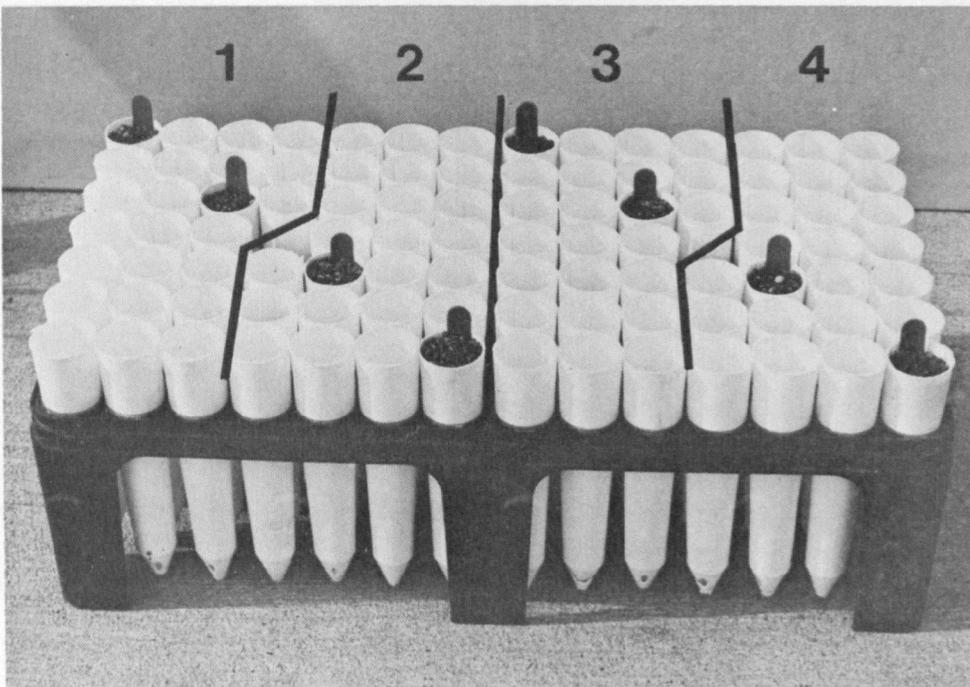


Figure 3. Rack filled with 96 cones, divided in four groups (1-4) of 24 cones each, representing one generation-replication. The tagged cones represent the control units, two such control cones were set in each generation-replication.

of 40 watts, which supplied between 800 and 900 fc (or between 8,600 and 9,700 lux) of light on the level where the seedlings were growing (64). Every month one tube was alternately replaced by a fresh one. This procedure assured that the light conditions were kept constant throughout the experiments.

Temperature

The temperature was maintained at 15 Celsius during the 12 hours of darkness and 21 C for the remaining 12 hours in light (64).

Growing Conditions

Plants were grown in a plastic container of 21 x 4 cm. Three small openings at the bottom of each container allowed excess water to leach out as well as for uptake of water via sub-irrigation. Five seeds were planted per container in a 50-50 mixture of clay and vermiculite as growth medium.

The following general procedure was followed during the research. Rotation was on a weekly schedule.

It took one week from planting to inoculation, and another week for the development of the powdery mildew until the seedlings could be read for their reaction type. For the first week the racks were kept on a greenhouse bench and watered daily. They were transferred to the growth chamber after inoculation on the seventh

day. On day 14, they were removed from the chamber for reading and were then replaced by a new series of freshly inoculated plants.

The Fungus, Erysiphe Graminis f.sp. Hordei

All the generations from the three CC populations were tested against the following four isolates of the barley powdery mildew fungus:

MT isolate: a Montana isolate collected from barley plots from the Horticultural Research Farm at Bozeman during the growing season of 1979. This isolate is very closely related to the CR3 race mentioned by Moseman (47, 49, 50, 52, 55, 57, 59). Culture CR3 is a single conidium subculture of the culture California race 3 (45).

59.11. The pathogenicity of culture 59.11 is typical of the pathogenic strains of the fungus isolated in commercial fields in northeastern U.S. and Ontario, Canada in 1958 (50, 52).

63.12. Culture 63.12 comes from England (52).

64.54. Culture 64.54 is an isolate from Israel.

The second, third and fourth isolates were received from the U.S.D.A. Laboratory of Dr. J. G. Moseman, in Beltsville, MD.

The selection of these four particular isolates was based on their response to the differential set for identification of physiologic races of E. graminis f.sp. hordei (46, 57). Twelve cultivars,

representing at least four loci were used in differential set (Table 8), and, after inoculation, these plants were read for their reaction types following the standard scale of reactions (Table 9).

It was desirable to test all the CC populations against several isolates of the fungus. The fungal cultures had to be different in virulence, so that the population response could be analyzed from different viewpoints. Three cultures were received from the U.S.D.A. laboratory in Beltsville, Maryland. With the Montana isolates, these cultivars represented a wide array of fungal origins and virulence levels. Young, inoculated barley seedlings were sent from Beltsville to Bozeman with moist soil around the roots to keep them alive during the three to four day trip. Immediately upon arrival the seedlings were transferred into pots until the fungus was fully developed, after which the powdery mildew was inoculated on the universal susceptible, Proctor (C.I. 11420), and on the differential set (Table 8). Then it was only a question of keeping the culture pure and alive, which was achieved by covering individual pots with lamp chimneys -- glass chimneys, 25 cm tall, or cellophane bags.

Only slight differences were detectable between these four cultures. The greatest differences were visible at the following loci:

Table 8. Reaction of 12 differential cultivars to four barley mildew isolates.^a

Variety		Host Genes	Mildew Isolates			
Name	C.I. No.		MT	59.11	63.12	64.54
1-Algerian	1179	M1-a+M1-at	0	0	0	0-0;
2-Rabat	4979	M1-a	0-0;	0	0	0-0;
3-Black Russian	2202	M1-a2	0;-1	4	1-3	1
4-Ricardo	6306	M1-a3	0;-1	4	1	1
5-Gopal	1091	M1-as,M1-a?	1	0-1	1	0;-1
6- <u>Hordeum spontaneum</u> <u>nigrum</u>	13130	M1-a6	0;-1	0	0	0
7-Gatersleben Mut.501	13132	M1-a6	0	0-1	0	1
8-Heil's Hanna	682	M1-a8	4	4	4	4
9-Cebada Capa	6193	M1-a?	1	2	2	4
10-Atlas	4118	M1-at	4	2	3/4	2-3
11-Goldfoil	928	M1-g	1	4	0-1	1
12-Chevron	1111	At or near M1-h locus	0/1	3	1	4

^aSee Table 9 for symbols used in reaction scale.

Table 9. Scale of reactions of barley seedlings to Erysiphe graminis f.sp. hordei. From Moseman (46).

0	No visible symptoms
0;	Very small flecks (mostly white)
1	Brown to purple flecks, with or without mycelia, having the appearance of necrotic flecks
2	Moderate sized pustules, with chlorosis and/or necrosis and mycelia growing
3	Large pustules with some necrosis or chlorosis
4	Large pustules with no chlorosis or necrosis
1-3	Mesothetic: reaction type 1 and 3 on the same leaf
1-4	Mesothetic: reaction type 1 and 4 on the same leaf

a-locus: M1-a2 and M1-a3 (cultivars Black Russian and Ricardo)

at-locus: M1-at (cultivar Atlas)

g-locus: M1-g (cultivar Goldfoil)

h-locus: M1-h (cultivar Chevron)

Inoculation Techniques

The powdery mildew fungus was kept alive by a weekly transfer from diseased plants to young, healthy seedlings by brushing the leaves against one another or by shaking the conidia over the healthy leaves. To enhance the production of young virulent conidia, the diseased pots were shaken slightly 24 hours before inoculation; this removed the older conidia from the conidiophore and whole chains of new fresh conidia were then produced.

Statistical Design and Working Methods

For each isolate, the following standard procedure was used:

1. Three racks, each containing 98 cones, fitted in one growth-chamber.
2. Each rack was divided into four sections of 24 cones each.

There were 22 cones for one replication of each generation and two cones for the control, Proctor. The remaining two spaces

were left empty to serve as border indicators (Figure 3). The controls were set in a diagonal throughout the halves of the rack. Each rack then was carrying four generation-replications. In each growth chamber there were 12 generation-replications present at all times, placed at random throughout each isolate-testing experiment. The overall experiment was a Completely Randomized Design.

3. Five seeds were planted in each cone. Thus, for each generation-replication there were $5 \times 22 = 110$ seedlings, and 2 x 5 or 10 check plants. Usually at least 100 seedlings could be read per generation-replication, and normally three replications were sufficient to produce 300 seedlings for each generation testing. But, as mentioned above, some generations had a lower germination percentage, and needed more replications (Table 7).
4. After seeding, the three racks were placed on a greenhouse bench and thoroughly watered on a daily basis for one week.
5. One week later, the three racks were inoculated by the use of heavily diseased plants grown for this purpose. Two pots with approximately 10 to 15 diseased seedlings were sufficient to inoculate the 480 plants of one rack. The three racks with the inoculated seedlings were then placed in the growth chamber

- for another week. During that week, the growth chamber was opened only once for observations and sub-irrigation.
6. One week after inoculation, each plant was read for its reaction type.
 7. After testing each isolate, the growth chamber was thoroughly cleaned with water and detergent. Test plants were grown to determine if any spores were still present.
 8. The seedlings were classified into two groups according to their reaction types:
 - A. The resistant group included all plants showing a non-compatible relationship with the powdery mildew culture, or those with a resistant or intermediate reaction type: 0 - 0; - 1 - 2 and 1/3.
 - B. The susceptible group included all plants with a compatible relationship with the fungus, and thus showing a susceptible reaction type: 3 - 4 and 1/4.

The number of resistant seedlings was computed for each treatment combination in each replication and computed to a percentage form. Statistical analyses were performed on these percentage data. An analysis of variance was computed for each population-isolate combination for each location. Duncan's multiple range test (76) was used to compare generation means within population-isolate combinations. Individual replication values were used for these

computations. For each population-isolate combination, percent resistant plants was regressed against generation number to determine if there was a significant linear relation between percent resistant plants (Y) and time (X). Individual replication values were used in the regression. Regression coefficients (b) were tested against zero using a t-test and the standard error of the regression was computed. The coefficient of determination (r^2) was calculated to explain the amount of variation accounted for by this linear relationship.

The expected frequency of resistant plants in the populations was calculated for each population-isolate combination following the initial synthesis of each CC population. For the calculations of this average expectancy, the following assumptions were made: 1) that resistance was conferred by one single dominant gene in each resistant parent; 2) that random sampling of alleles for resistance occurred when the crosses were made; and 3) that random mating was achieved during the formation of each composite.

RESULTS

Composite Cross II

Parents

The genetic basis for resistance of five parents (Algerian, Atlas, Lyallpur, Multan and Palmella Blue) which possess resistance to one or more of the E. graminis cultures studied are shown in Table 3.

The reaction types of the 28 parents to the four isolates of E. graminis f.sp. hordei are presented in Table 10. No seed could be found of the cultivar Orel (C.I. 351).

From the 28 parents that formed this CC population, five were found to have a resistant reaction type to the isolate MT, five to 63.12, six to 64.54, and eight to 59.11. Algerian, Multan and Palmella Blue were resistant to all four cultures.

Other resistant reactions were: 1) MT on Lion and Lyallpur; 2) 59.11 on Lion, Lyallpur, Arequipa, Atlas and Meloy; 3) 63.12 on Lyallpur and Meloy; and 4) 64.54 on Lion, Everest and Flynn. These results indicate that the four cultures are different in virulence. Also, culture 59.11 is the least virulent of the four isolates, followed by 64.54 and by MT and 63.12.

Table 10. Known genetic constitution of the 28 parents of composite cross II and their reaction types to the four cultures of *E. graminis* used in this experimental study.

Cultivar	C.I.	Mildew Gene ^b	<i>Erysiphe graminis</i> f.sp. <i>hordei</i> culture ^a			
			MT	59.11	63.12	64.54
1-Algerian	1179	<u>M1-a+M1-at</u>	0(R) ^c	0(R)	0(R)	0/0;(R)
2-Alpha	959		4	4	4	4
3-Arequipa	1256		4	2(R)	4	4
4-Atlas	4228	<u>M1-at</u>	4	2(R)	3/4	2-3
5-California Mariout	3625		4	4	4	4
6-Club Mariout	261		3/4	4	4	4
7-Everest	4105		4	4	4	0/0;(R)
8-Flynn	1311		4	4	4	1/2(R)
9-Glabron	4577		4	4	4	4
10-Golden Pheasant	2488		4	4	4	4
11-Good Delta	3801		4	3	4	4
12-Hannchen	531		4	4	4	4
13-Han River	206		4	4	4	4
14-Horn	926		4	4	4	4
15-Lion	2238		1(R)	2(R)	3/4	1/2(R)
16-Lyallpur	3403		2(R)	1(R)	0/1(R)	4
17-Maison Carree	3387		4	4	4	4
18-Manchuria	2330		4	4	3/4	4
19-Meloy	1176		4	1/2(R)	2(R)	4
20-Minia	3556		4	4	4	4
21-Multan	3401	<u>M1-a?</u>	0;/1(R)	0;/1(R)	1(R)	0/1(R)
22-Oderbrucker	4666		4	4	3/4	4
23-Orel	351		?	?	?	?
24-Palmella Blue	3609	<u>M1-a?+M1-g?</u>	0(R)	1(R)	1(R)	1(R)
25-Sandrel	937		4	4	4	4
26-Trebi	936		4	4	4	3/4
27-White Smyrna	910		4	4	4	4
28-Wisconsin Winter	2159		4	4	4	4
Number of resistant parents			5	8	5	6
Expected frequency of resistant germplasm ^d			18%	28%	18%	21%

^a See Table 9 for the symbols used in the reaction scale.

^b See Table 3 for the genetic background information.

^c (R) = Resistant

^d See Materials and Methods, for assumptions made in calculations.

Composite Cross II at Three Locations

CC II, California (Table 11 and Figure 4)

None of the regression coefficients were significantly different from zero. There was no steady increase or decrease in the frequency of plants resistant to the four isolates tested from generation eight to generation 51.

Significant differences among generation means were found only for cultures 59.11 and 64.54. Twenty to 40% resistant seedlings were detected by inoculations with culture 59.11, while 13% or less resistance was detected by inoculations with culture MT.

CC II, Moccasin (Table 12 and Figure 5)

Only three generations from this population were available for evaluation.

None of the regression coefficients were significantly different from zero. Significant differences among generation means were found only for isolate 64.54. An irregular pattern was observed in the frequency of resistant plants in the population as a result of inoculations with culture 64.54. There were differences in the frequency of resistance observed among the F20, the F13 and the F35 generations, respectively.

Table 11. Frequency means and regression statistics of the percentage of plants resistant to four cultures of Erysiphe graminis f.sp. hordei over five generations of CC II from California.

Generation	Isolate			
	MT	59.11	63.12	64.54
FREQUENCY MEANS*				
F 8	3.8 a	39.3 b	15.6 a	8.1 a
F 16	1.6 a	31.7 ab	25.4 a	17.0 ab
F 26	4.5 a	31.9 ab	13.0 a	4.7 a
F 48	0.7 a	23.1 a	10.2 a	2.9 a
F 51	13.1 a	37.1 b	26.8 a	24.4 b
Expected frequency	18.0	28.0	18.0	21.0
REGRESSION				
r^2 (%)	8	11	0	2
b	0.114	-0.114	0.010	0.088
S.E.	0.110	0.108	0.116	0.170

*Means within columns of each isolate-composite cross combination followed by the same letter are not significantly different from each other, $P = 0.05$, by Duncan's multiple range test.

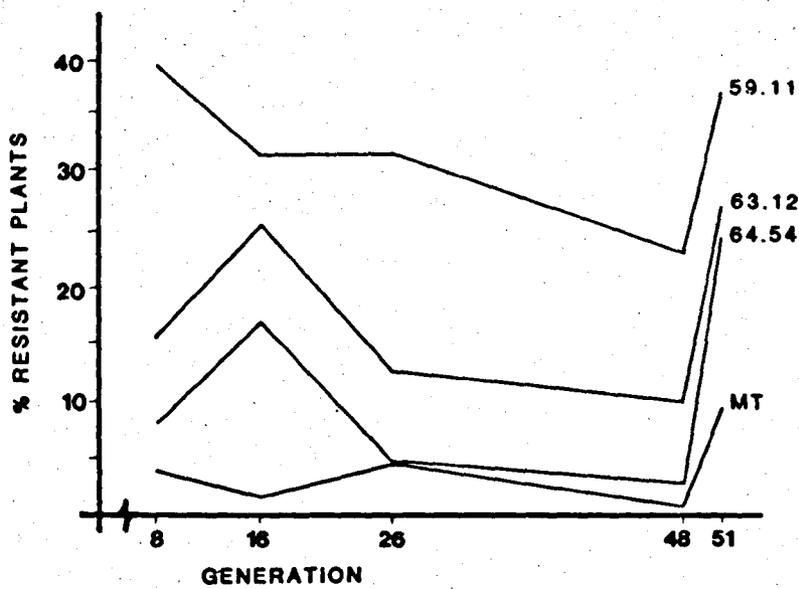


Figure 4. Percentage of plants resistant to four cultures of *Erysiphe graminis* f.sp. *hordei* over five generations of Composite Cross II from California.

Table 12. Frequency means and regression statistics of the percentage of plants resistant to four cultures of Erysiphe graminis f.sp. hordei over three generations of CC II from Moccasin.

Generation	Isolate			
	MT	59.11	63.12	64.54
<u>FREQUENCY MEANS*</u>				
F 13	7.7 a	17.3 a	10.4 a	7.5 a
F 20	7.5 a	21.6 a	11.6 a	21.7 b
F 25	9.7 a	14.2 a	9.8 a	10.9 ab
Expected frequency	18.0	28.0	18.0	21.0
<u>REGRESSION</u>				
r ² (%)	13	2	26	6
b	0.175	-0.202	0.877	0.397
S.E.	0.182	0.478	0.518	0.559

*Means within columns of each isolate-composite cross combination followed by the same letter are not significantly different from each other, P = 0.05, by Duncan's multiple range test.

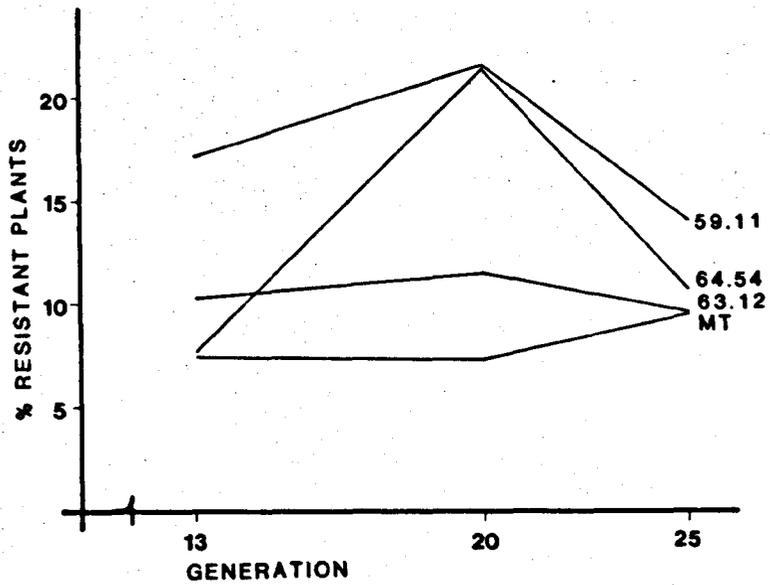


Figure 5. Percentage of plants resistant to four cultures of Erysiphe graminis f.sp. hordei over three generations of Composite Cross II from Moccasin.

Inoculations with culture 59.11 resulted in the largest number resistant plants, while inoculations with culture MT showed the smallest frequencies of resistant individuals.

CC II, Bozeman (Table 13 and Figure 6).

Significant differences between the generation means were detected for culture 59.11 only. The percentage of resistant plants increased from 39 to 57% in the short period from the F26 to the F37. A positive and significant linear relationship was found between the percentage of resistant plants and the three generations of this composite inoculated with culture 59.11.

Culture 59.11 was the least virulent, while isolate MT was so widely virulent that only a few resistant plants could be detected in the population.

Composite Cross V

Parents

In this cross, the genetic basis for resistance is known only in Algerian and Atlas (Tables 3 and 4). The cultivars Algerian and Atlas were also included in CC II.

The reaction types of these 30 cultivars to the four cultures of the powdery mildew fungus used in these experiments is presented

Table 13. Frequency means and regression statistics of the percentage of plants resistant to four cultures of Erysiphe graminis f.sp. hordei over three generations of CC II from Bozeman.

Generation	Isolate			
	MT	59.11	63.12	64.54
<u>FREQUENCY MEANS*</u>				
California F 26	4.5	31.9	13.0	4.7
F 26	2.9 a	39.2a	14.8 a	11.8 a
F 31	0.3 a	51.8 b	17.7 a	11.5 a
F 37	1.0 a	57.4 b	7.2 a	15.7 a
Expected frequency	18.0	28.0	18.0	21.0
<u>REGRESSION</u>				
r ² (%)	19	73	20	4
b	-0.163	1.63**	-0.714	0.335
S.E.	0.126	0.374	0.583	0.652

*Means within columns of each isolate-composite cross combination followed by the same letter are not significantly different from each other, P = 0.05, by Duncan's multiple range test.

**Regression is significant at the 1% level.

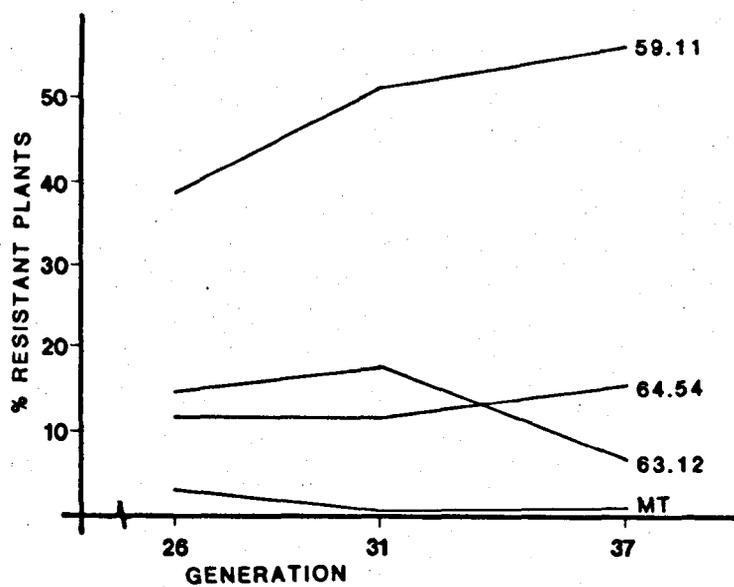


Figure 6. Percentage of plants resistant to four cultures of Erysiphe graminis f.sp. hordei over three generations of Composite Cross II from Bozeman.

in Table 14. CC V has eleven cultivars in common with CC II. Eight parents were found to be resistant to culture 59.11, five to culture 64.54, and four to the other two cultures. The most resistant plants were revealed in the composite after inoculation with culture 59.11. The isolates are different from each other in their infection types on the parents. Only Algerian was resistant to all four isolates. In addition, resistant reactions were shown as follows: 1) MT on Afghan II, Abate and Lion; 2) 59.11 on Abate, Arequipa, Black Algerian, Coaston, Lion and Old ZZ (ZZ first); 3) 63.12 on Afghan II, Abate and Coaston; and 4) 64.54 on Lion, Vaughn, and Flynn.

Composite Cross V at Three Locations

CC V, California (Table 15 and Figure 7)

Significant differences between the generation means were detected for the cultures MT, 59.11 and 63.12. For culture 63.12 there was also a positive and significant relationship between the percentage resistant seedlings and generations.

CC V, Moccasin (Table 16 and Figure 8)

Significant differences between the percentage of resistant plants of the two generations tested were found for all the isolates except for isolate 63.12.

Table 14. Known genetic constitution of the 30 parents of composite cross V and their reaction types to the four cultures of *E. graminis* f.sp. *hordei* used in this experimental study.

Cultivar	C.I.	Mildew Gene ^b	<i>Erysiphe graminis</i> f.sp. <i>hordei</i> cultures ^a			
			MT	59.11	63.12	64.54
1-Abate	14119		0/0;(R) ^c	2(R)	1/2(R)	3/4
2-Afgan I	4166		4	4	3/4	4
3-Afghan II	6366		0/0;(R)	4	0;(R)	3/4
4-Algerian	1179	Ml-a+Ml-at	0(R)	0(R)	0(R)	0/0;(R)
5-Arequipa	1256		4	2(R)	4	4
6-Atlas	4118	Ml-at	4	2(R)	3/4	2/3
7-Baker	975		4	4	4	4
8-Black Algerian	708		3/4	4	4	1/2(R)
9-Bonfarik	14061		4	4	4	2/4
10-Club Mariout	261		3/4	4	4	4
11-Coaston	6626		4	2(R)	2(R)	4
12-Ezond	6265		4	4	4	4
13-Flynn	13115		4	4	4	1/2(R)
14-Goodwill	6083		4	4	4	4
15-Han River	206		4	4	4	4
16-Lion	2238		1(R)	2(R)	3/4	1/2(R)
17-Lioness	4019		4	4	4	4
18-Maison Caree	3387		4	4	4	4
19-Minia	3556		4	4	4	4
20-New ZZ (ZZ second)	6299		4	4	2/3	4
21-Old ZZ (ZZ first)	6298		4	2(R)	2/3	4
22-Pannier	1330		3/4	4	4	3/4
23-Parla	14065		4	4	3/4	3
24-Pestland	5267		4	3	4	4
25-Rikote	5888		4	4	4	4
26-Sandrel	937		4	4	4	4
27-Stavropol	2103		4	4	3/4	3/4
28-Trebi	936		4	4	4	3/4
29-Vaughn	1367		4	4	4	1/2(R)
30-Velvon	6109		4	4	4	4
Number of resistant parents			4	8	4	5
Expected frequency of resistant germplasm ^d			13%	26%	13%	17%

^a See Table 9 for the symbols used in the reaction scale.

^b See Table 3 for the genetic background information.

^c (R) = Resistance.

^d See Materials and Methods for assumptions made in calculations.

Table 15. Frequency means and regression statistics of the percentage of plants resistant to four cultures of Erysiphe graminis f.sp. hordei over five generations of CC V from California.

Generation	Isolate			
	MT	59.11	63.12	64.54
<u>FREQUENCY MEANS*</u>				
F 6	7.0 b	28.1 b	7.3 a	13.5 a
F 13	6.6 b	27.2 b	8.2 ab	9.9 a
F 24	14.0 c	17.9 a	16.1 ab	15.4 a
F 33	5.4 ab	28.5 b	25.8 b	18.1 a
F 36	1.5 a	33.5 b	17.0 ab	9.5 a
Expected frequency	13.0	26.0	13.0	17.0
<u>REGRESSION</u>				
r^2 (%)	8.0	3.0	30.0	1.0
b	-0.115	0.122	0.478**	0.049
S.E.	0.104	0.163	0.194	0.133

*Means within columns of each isolate-composite cross combination followed by the same letter are not significantly different from each other, $P = 0.05$, by Duncan's multiple range test.

**Regression is significant at the 5% level.

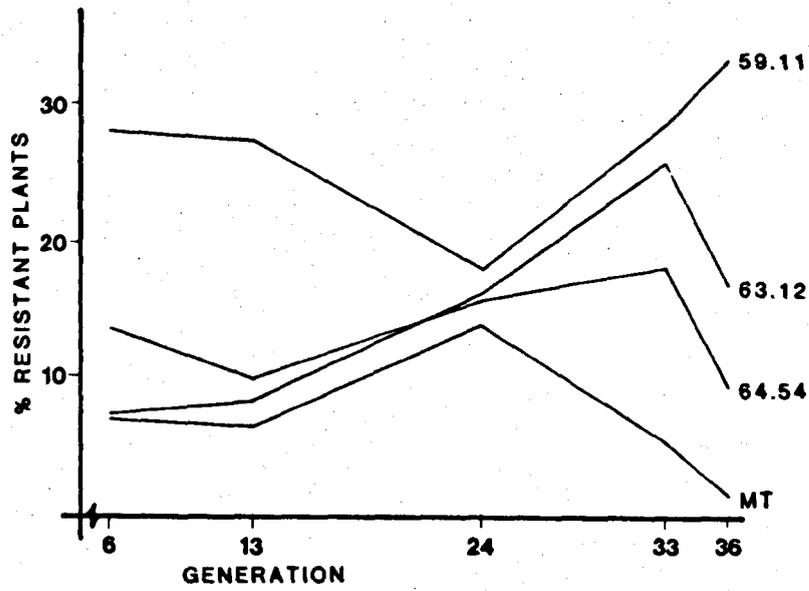


Figure 7. Percentage of plants resistant to four cultures of *Erysiphe graminis* f.sp. *hordei* over five generations of Composite Cross V from California.

Table 16. Frequency means and regression statistics of the percentage of plants resistant to four cultures of Erysiphe graminis f.sp. hordei over two generations of CC V from Moccasin.

Generation	Isolate			
	MT	59.11	63.12	64.54
FREQUENCY MEANS*				
F 12	8.9 a	30.9 a	11.8 a	20.6 a
F 20	2.1 b	17.8 b	18.5 a	7.1 b
Expected frequency	13.0	26.0	13.0	17.0

*Means within columns of each isolate-composite cross combination followed by the same letter are not significantly different from each other, P = 0.05, by Duncan's multiple range test.

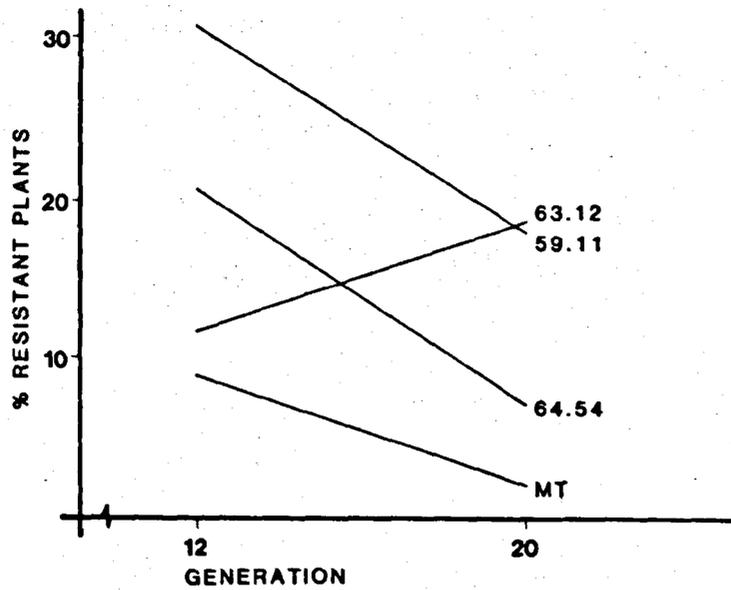


Figure 8. Percentage of plants resistant to four cultures of *Erysiphe graminis* f.sp. *hordei* over two generations of Composite Cross V from Moccasin.

There was a great reduction in frequency of resistance that occurred within the populations between the F12 and the F20 generations for all the cultures except for 63.12. It is also the first time that culture 59.11 showed such a sharp decline in frequency of resistance. However, culture 59.11 remained the least virulent isolate and all fluctuations were on the order of 10%.

CC V, Bozeman (Table 17 and Figure 9)

No significant differences between the generation means were detected after inoculation with the four powdery mildew cultures.

Composite Cross XII

Parents

Composite cross XII is closely related to CC V. The known resistance genes of two parents (Atlas and Chevron) with resistance to one or more of the E. graminis cultures studied are shown in Tables 3 and 18. Atlas was also found in CC V.

The reaction types of these 25 cultivars to the four fungal cultures are presented in Table 18. Abate, Afghan II, Arequipa, Atlas, Black Algerian, Chevron, Coaston, Flynn, Lion and Vaughn have resistance to at least one culture of the fungus. Of these 11 parents, CC V differed from CC XII only in the cultivar Algerian. CC XII has the resistant parent Chevron. Algerian in CC V was resistant to all the isolates, while the cultivar Chevron resisted

Table 17. Frequency means and regression statistics of the percentage of plants resistant to four cultures of *Erysiphe graminis* f.sp. *hordei* over three generations of CC V from Bozeman.

Generation	Isolate			
	MT	59.11	63.12	64.54
FREQUENCY MEANS*				
F 5	6.4 a	29.0 a	10.2 a	13.5 a
F 9	7.4 a	28.5 a	6.7 a	6.2 ab
F 14	9.6 a	25.1 a	10.8 a	16.0 b
Expected frequency	13.0	26.0	13.0	17.0
REGRESSION				
r ² (%)	26	11	0.9	11
b	0.362	-0.426	0.093	0.499
S.E.	0.231	0.424	0.37	0.565

*Means within columns of each isolate-composite cross combination followed by the same letter are not significantly different from each other, P = 0.05, by Duncan's multiple range test.

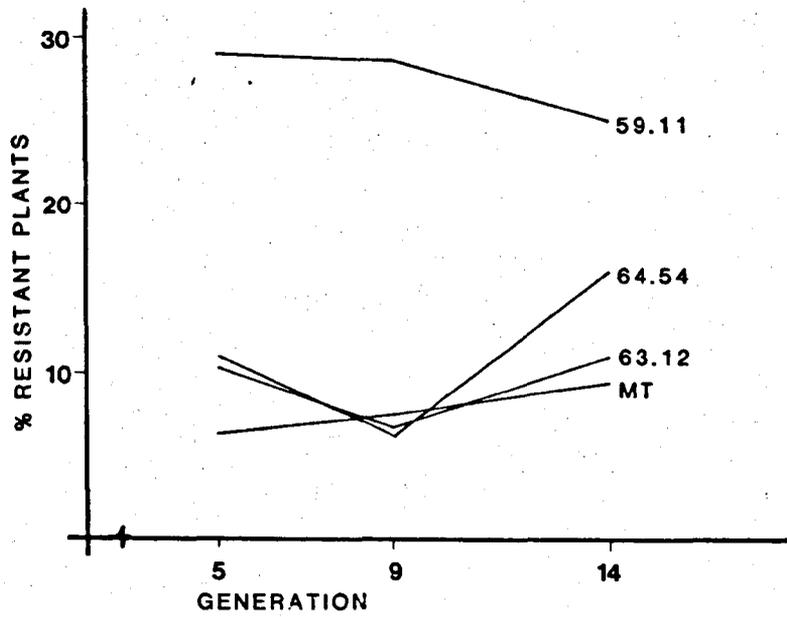


Figure 9. Percentage of plants resistant to four cultures of *Erysiphe graminis* f.sp. *hordei* over three generations of Composite Cross V from Bozeman.

Table 18. Known genetic constitution of the 25 parents of composite cross XII and their reaction types to the four cultures of *E. graminis* f.sp. *hordei* used in this experimental study.

Cultivar	C.I.	Mildew Gene ^b	Erysiphe graminis f.sp. hordei cultures ^a			
			MT	59.11	63.12	64.54
1-Abate	14119		0/0;(R) ^c	2(R)	1/2(R)	3/4
2-Afghan I	4166		4	4	3/4	4
3-Afghan II	6366		0/0;(R)	4	0;(R)	3/4
4-Arequipa	1256		4	2(R)	4	4
5-Atlas	4118	<u>M1-at</u>	4	2(R)	3/4	2/3
6-Black Algerian	708		3/4	2(R)	4	1/2(R)
7-Bolivia	1257		4	3	3/4	4
8-Bonfarik	14061		4	4	4	2/4
9-Chevron	1111	<u>M1-h</u>	0/1(R)	3	1(R)	4
10-Club Mariout	261		3/4	4	4	4
11-Coaston	6626		4	2(R)	2(R)	4
12-Ezond	6265		4	4	4	4
13-Flynn	13115		4	4	4	1/2(R)
14-Lion	2238		1(R)	2(R)	3/4	1/2(R)
15-Lioness	4019		4	4	4	4
16-Maison Caree	3387		4	4	4	4
17-Minia	3556		4	4	4	4
18-Old ZZ (ZZ first)	6298		4	2(R)	2/3	4
19-Olli	6251		4	4	3	3/4
20-Parla	14065		4	4	3/4	3
21-Rikote	5889		4	4	4	4
22-Sandrel	937		4	4	4	4
23-Trebi	936		4	4	4	3/4
24-Vaughn	1367		4	4	4	1/2(R)
25-Velvon	6109		4	4	4	4
Number of resistant parents			4	7	4	4
Expected frequency of resistant germplasm ^d			11%	41%	9%	34%

^a See Table 9 for the symbols used in the reaction scale.

^b See Table 3 for the genetic background information.

^c (R) = Resistant.

^d See Materials and Methods for assumptions made in calculations.

cultures MT and 63.12. Seven of the parents were resistant to culture 59.11. Four parents were resistant to the other three cultures.

Composite Cross XII at Three Locations

CC XII, California (Table 19 and Figure 10)

There were significant differences among generation means for all isolates except 64.54.

Resistance to cultures 63.12 and MT exhibited a gradual increase over the generations.

For culture 63.12, a 19% increase in the frequency of resistant plants was observed from the F6 to the F35. The relationship found was positive and significant. The linear relationship was also positive and significant for culture MT, with a 17% increase in resistance from the F6 to the F35. No significant increase in frequency of resistant plants was observed after inoculations with cultures 59.11 and 64.54.

CC XII, Moccasin (Table 20 and Figure 11)

Significant differences between the percentage of resistant plants of the two generations tested were revealed for the isolates

Table 19. Frequency means and regression statistics of the percentage of plants resistant to four cultures of *Erysiphe graminis* f.sp. *hordei* over five generations of CC XII from California.

Generation	Isolate			
	MT	59.11	63.12	64.54
<u>FREQUENCY MEANS*</u>				
F 6	5.2 a	32.5 ab	13.2 a	16.3 a
F 16	14.2 bc	32.4 ab	18.5 ab	13.4 a
F 24	19.0 cd	20.7 a	25.3 bc	11.0 a
F 29	12.4 b	20.3 a	28.2 bc	8.1 a
F 35	22.6 d	34.3 b	32.5 c	20.8 a
Expected frequency	11.0	41.0	9.0	34.0
<u>REGRESSION</u>				
r^2 (%)	58.0	4.0	69.0	0.4
b	0.486**	-0.166	0.678**	0.044
S.E.	0.113	0.214	0.125	0.186

*Means within columns of each isolate-composite cross combination followed by the same letter are not significantly different from each other, $P = 0.05$, by Duncan's multiple range test.

**Regression is significant at the 1% level.

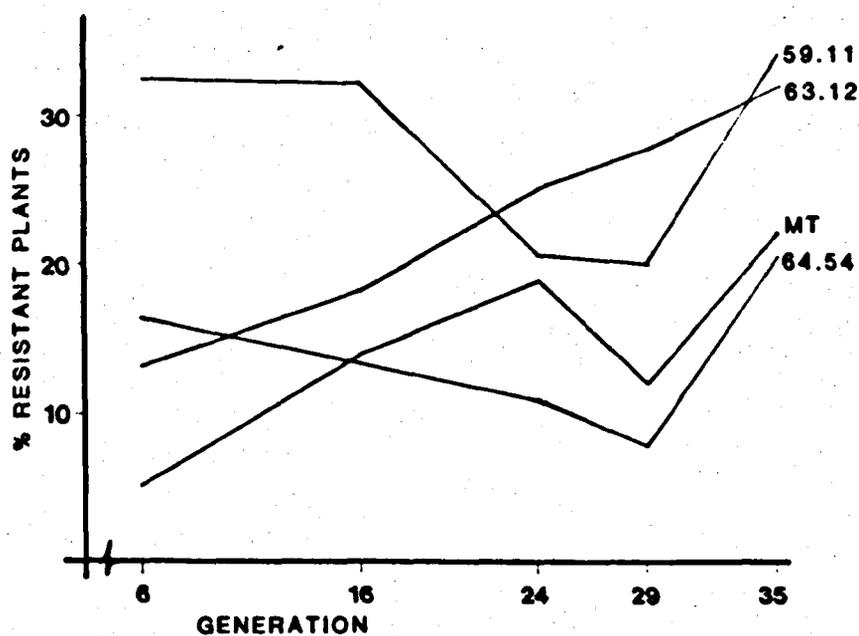


Figure 10. Percentage of plants resistant to four cultures of *Erysiphe graminis* f.sp. *hordei* over five generations of Composite Cross XII from California.

MT and 59.11. However, where there was a 23% increase in resistance in this population to culture 59.11, while a steady decline of about 8% for culture MT was observed.

No significant changes in resistance between the generations tested were found for 64.54 and 63.12.

CC XII, Bozeman (Table 21 and Figure 12)

No significant differences were found in the frequency of resistant plants in the F7, F9 and F12 of this population for three of the four isolates. Only for culture 59.11 was a significant difference in resistance over the generations observed. The frequency of resistant plants increased constantly from about 30% to 50% from the F7 to F14 for isolate 59.11.

The regression coefficient was positive and significantly different from zero ($P < 0.025$).

Table 20. Frequency means and regression statistics of the percentage of plants resistant to four cultures of Erysiphe graminis f.sp. hordei over two generations of CC XII from Moccasin.

Generation	Isolate			
	MT	59.11	63.12	64.54
FREQUENCY MEANS*				
F 6	10.1 a	23.9 a	7.7 a	11.6 a
F 20	20.0 b	46.9 b	9.5 a	8.3 a
Expected frequency	11.0	41.0	9.0	34.0

*Means within columns of each isolate-composite cross combination followed by the same letter are not significantly different from each other, P = 0.05, by Duncan's multiple range test.

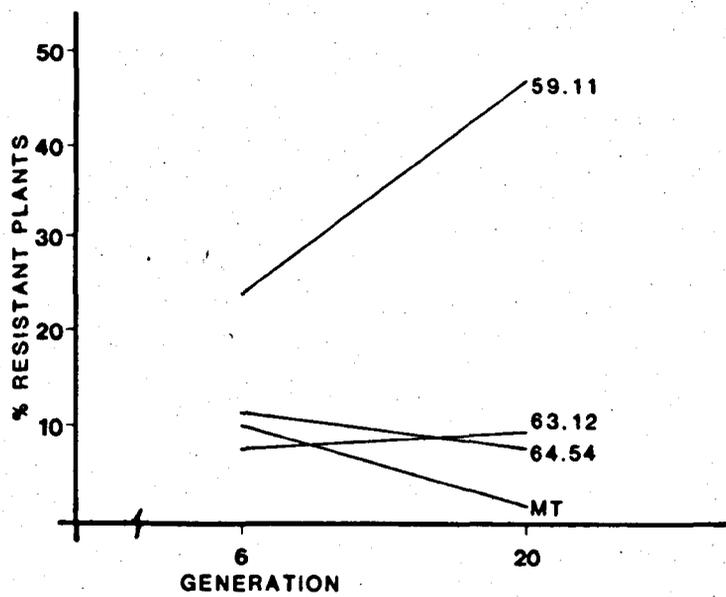


Figure 11. Percentage of plants resistant to four cultures of Erysiphe graminis f.sp. hordei over two generations of Composite Cross XII from Moccasin.

Table 21. Frequency means and regression statistics of the percentage of plants resistant to four cultures of *Erysiphe graminis* f.sp. *hordei* over three generations of CC XII from Bozeman.

Generation	Isolate			
	MT	59.11	63.12	64.54
FREQUENCY MEANS*				
F 7	3.6 a	32.7 a	8.9 a	12.4 a
F 9	1.0 a	36.3 ab	9.0 a	15.4 a
F 14	2.4 a	47.6 b	7.9 a	14.5 a
Expected frequency	11.0	41.0	9.0	34.0
REGRESSION				
r^2 (%)	0.6	57	0.9	1.3
b	-0.08	2.158**	-0.153	0.198
S.E.	0.402	0.707	0.609	0.633

*Means within columns of each isolate-composite cross combination followed by the same letter are not significantly different from each other, $P = 0.05$, by Duncan's multiple range test.

**Regression is significant at the 5% level.

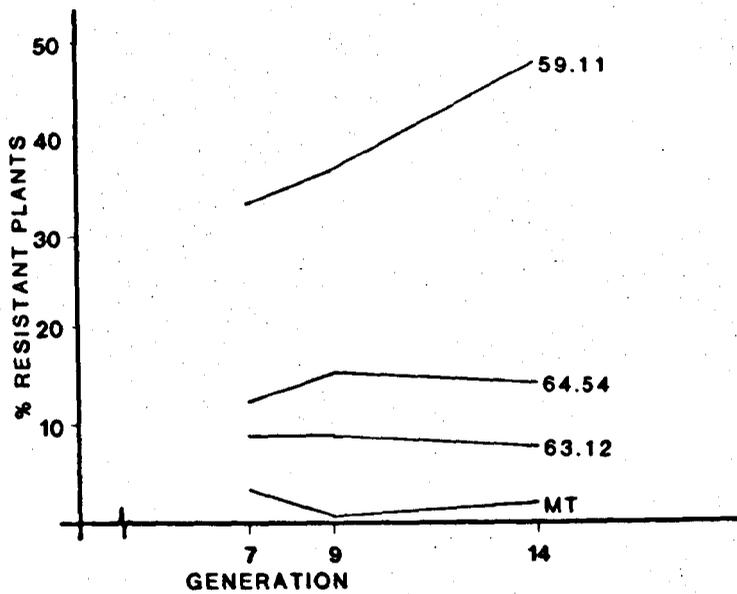


Figure 12. Percentage of plants resistant to four cultures of *Erysiphe graminis* f.sp. *hordei* over three generations of Composite Cross XII from Bozeman.

DISCUSSION

The Environment

Powdery mildew occurs wherever barley is grown. In California, it is one of the most important diseases (68). Selective influence from powdery mildew on the CC populations developed at Davis, California, can be expected during certain years of heavy continuous fungal infection throughout the growing season. Selective influence of powdery mildew is not expected in Montana, because powdery mildew occurs only early in the season and the infection usually does not progress beyond the lower leaves.

Influence of the Pathogen Cultures

Four cultures of *E. graminis* f.sp. *hordei* that differed in origin and virulence were used in this study. In the tests of the parents of each CC population, the greatest amount of resistance in the hosts was revealed by culture 59.11. Twenty-six percent of the parents of CC V, 28% of the parents of CC II and 40% of those of CC XII had resistance to culture 59.11 (Tables 10, 14, 18). Culture 64.54 revealed less resistance than culture 59.11, but more than the other two cultures MT and 63.12.

Eighteen percent of the parents of CC II, 13% of the parents of CC V and about 10% of those of CC XII had resistance to the cultures MT

and 63.12 (Tables 10, 14, 18). Cultures MT and 63.12 were thus the most virulent isolates in the tests of the parents that formed the composites.

Selection

In only five out of the 36 generation-isolate combinations were significant increases in the frequency of resistant plants found in response to inoculations with the powdery mildew cultures. These were:

1. Bozeman CC II to culture 59.11. An 18% increase in resistance was found in the period of 11 years from the F26 to F37. This increase was higher than the calculated expected frequency of resistance (Table 12).
2. Moccasin CC XII to culture 59.11. A 23% increase in resistance was found from the F6 to the F20. The frequency of resistant plants over the generations was, however, equal to the calculated expectancy (Table 20).
3. Bozeman CC XII to culture 59.11. The 15% increase in frequency of resistant plants from the F7 to the F14 was equal to the calculated expected frequency (Table 21).
4. California CC XII. Culture 63.12 showed a 19% increase and culture MT an 18% increase in resistance from the F6 to the F35.

In both cases, the increase was higher than the respective calculated expectancy (Table 19).

The greatest increase in frequency of resistance were detected by inoculations with culture 59.11. Also, CC XII, at the three locations, revealed the most and the largest increases in resistant plants of the three populations. In these instances selection pressure might have been applied by the pathogen to the populations. After such host-pathogen interactions, the barley CC populations may have responded to the selection pressure by favoring plants resistant to the fungus. However, in all the other population-isolate tests, no such significant changes in resistance frequency were observed. Mostly random variations and random changes in frequency were revealed.

While resistance was maintained throughout the generations in all the population-isolate testings, it was not always preserved at the original parental levels. In some instances, less resistance was detected than the calculated expectancy, such as in the Bozeman CC II and CC XII to culture MT and in CC XII at the three locations to 64.54. Sometimes, resistance was reduced, the frequency of resistant plants decreasing over the generations to a lower level than the expected frequency, such as in the CC V and CC XII from California and Moccasin to culture MT.

Few general conclusions can be deduced from these results because too many random variations were observed for each culture tested. Increases in frequency of resistance were expected from the populations grown in California as compared to the same populations grown in Montana. Overall, resistance to powdery mildew was conserved in the California populations more consistently than in the Montana populations. When the expected frequency of resistance was compared to the frequency of resistant plants in the subsequent generations of each CC population, the difference between California and Montana conditions became apparent. However, the Montana populations did not lose all their resistance to powdery mildew, since in all tests some levels of resistance were detected.

It is unlikely that the few increases in resistance that occurred in these testings resulted solely from selection pressure imposed by powdery mildew. Suneson and Stevens (80) in their studies with CC II concluded that disease resistance to scald in California was not a potent factor in survival of a bulked hybrid population of barley. On the other hand, Jackson, et al. (26) found drastic increases in the frequency of plants resistant to scald in CC II, one of three populations tested. They suggested that alleles governing specific resistance to scald were associated with other adaptive gene complexes in certain parents of CC II. These gene complexes were

postulated to confer selective advantage in the subsequent generations of CC II and the resistant alleles were pulled along as selection caused these gene complexes to increase in frequency in the population. The same explanation could possibly explain the erratic results obtained in this study with the different population-powdery mildew isolate combinations. Genetic variability within and among populations is governed mainly by the combined effects of mutation, selection, migration, genetic drift and mating system. Allard, et al. (3) showed that changes in gene and genotypic frequencies at four esterase loci over 25 generations of CC V were not due to mutation, migration or genetic drift. Selection and mating system were responsible for the observed changes in gene and genotypic frequencies in CC V. Selection operated differentially on the four tightly linked loci of the study. Allard, et al. (3) stated:

"These results lead us to the conclusion that the observed patterns of enzymatic variation in CC V result from balancing selection with strong selection intensities and with the direction of selection different for various alleles."

There is also evidence that heterozygotes occur in excess in these barley populations over expectations based on mating system alone (3, 13, 84) and also that the excess of heterozygotes increases over the generations in CC V (38). Mating systems are an important determinant of population structure because they affect the recombinational potential of populations, changing the rate of production

or breakdown of gene combinations (38). Reproduction in barley is usually one of 99% self-fertilization and about 1% outcrossing. In CC V, Kahler, et al. (38) found that the outcrossing rate had increased significantly from an average of 0.57% in the F8 to 1.24% in the F28. They also found evidence for selection during the reproductive phases of the life cycle of populations. Heterozygotes were about 52% superior to homozygotes in reproductive capacity (84).

Examination of two locus zygotic arrays in CC V by Weir, et al. (84) indicated that each allele at any one locus was favored in at least one combination, and was at a disadvantage in at least one combination with alleles at each other locus. They found evidence for complex epistatic nature of the selective forces acting upon barley CC populations. Weir, et al. (84) concluded: "The complex behavior of these four enzyme loci in the population is attributed to interactions between selection and restriction of recombination resulting from the effects of linkage and/or inbreeding." Clegg, et al. (13) found a buildup of striking correlations between loci, including nonlinked loci, and evidence for selection that was operating on these coadapted multilocus units. Epistatic selection might also be the explanation for the positive correlations found between resistance to three of the four isolates of scald used in a study by Muona, et al. (62) on CC II. Epistatic selection would have developed

gametic disequilibrium between favored combinations at different genetic loci in inbreeding populations.

It is clear then that natural selection was the primary force responsible for the organization of the genetic materials in highly correlated units (13). The above studies indicated that different types of selection can be involved in the formation and maintenance of coadapted blocks of genes.

In this study of powdery mildew interactions with three barley CC populations, it was possible that alleles for specific resistance in barley were associated with traits that had a selective advantage. This would explain the few cases where increases occurred in the frequency of resistant plants over the generations. Barley CC populations have developed highly organized population structures with coadapted gene complexes, where nonrandom associations at different genetic loci occurred (13, 84). It is possible that alleles for specific resistance to powdery mildew were associated with such gene complexes in these three CC populations. Selection acting upon these gene complexes could have caused them to increase in frequency over the generations. An examination of possible marker genes or loci and their occurrences at several stages in the population might explain the trends found in these results.

The hordein loci were the only markers found to be in close association with some known powdery mildew genes. The recombination

percentage between Ml-k and Hor 1 was estimated to be 4.0 ± 1.3 , between Hor 1 and Ml-a, 5.3 ± 1.1 , and between Ml-a and Hor 2, 6.1 ± 1.2 (33, Appendices 1 and 2). This close association of these hordein loci with some genes for resistance to powdery mildew renders them very useful as marker genes (15). Doll and Brown (15) investigated hordein variation in a CC population. They were able to deduce from hordein variation in CC XXI that the frequency of the Atlas phenotype in the F17 was not as high as was expected previously. They concluded (15): "It is clear that storage protein furnishes a very useful basis for varietal identification and for evolutionary studies." A study on these hordein loci and their evolution in other CC populations would be an interesting follow-up for this research, because of their close association with the powdery mildew resistance genes Ml-a and Ml-k.

Whatever the mode of selection is, it is a primary force acting upon the genetic materials in these CC populations. Selection was operating during all the life cycle stages of the population with different intensity and direction (14).

Genetic Variation

The three CC populations which were the object of this experimental study were grown at three different locations under natural selection. In this barley-powdery mildew ecosystem, the pathogen was

confronted by a great diversity in barley genotypes. Largely homozygous plants were competing with each other in a heterogeneous mixture. The reaction of each of these individuals to powdery mildew was affected by this competition.

This study was performed on seed samples from which approximately 300 seedlings were tested in each generation-isolate combination (Table 7). The seed samples may or may not have reflected the behavior of the population as a whole. For example, one sample might have contained a larger proportion of heterozygote or segregating individuals than that actually are present in the population. The same can be said for the parental material, received from Beltsville, Maryland. One might argue if these cultivars were still identical to the original parents that made up those populations. In both cases this variation would have resulted in different reactions to the disease.

The powdery mildew fungus also has genetic variations, and would adapt itself to changes occurring within the host population. Therefore, when a number of host genotypes (cultivars) are tested against a number of pathogen genotypes (isolates), the genetic variation in the resulting disease assessment can be dependent or independent.

Dependent genetic variation is specific variation, and a significant interaction occurs between cultivars and isolates. Dependent

variation in host resistance results from variation in pathogenicity of the powdery mildew fungus. That is, the ranking of cultivars for resistance depends upon the pathogen isolate used. This can be referred to as race-specific or vertical resistance (66, 82).

On the other hand, with general, race non-specific, horizontal resistance, independent genetic variation occurs, and the rankings of cultivars is the same for all the isolates. Host resistance varies independently of the pathogenicity in the pathogen (66, 82).

The data presented here were the results of investigations on race-specific interactions only. Independent genetic variation can be measured in other ways which were not the subject of this study.

One must emphasize that this reasearch was conducted on one aspect of the total genetic interactions which occur in CC populations. It was conceived, however, to be another analysis of one of the many components involved in population genetics. One must look at associations with other gene complexes for an adequate answer to increased resistance over time.

Concluding Remarks

The results of the present study serve to accentuate the many beneficial aspects of population breeding. Population breeding is not usually a goal in itself, but is an integral part in a breeding program. Every plant breeder today needs to remember that his crop

plants are always subject to natural selection that operates in a directional way. The original composition of the mixture is very important. "The genes that one puts in the population initially will be maintained in the population during the many generations of its existence" notes Allard (personal communication). Moreover, some very interesting recombinants may originate from the population. The bulk composite population contains a fantastic amount of genetic variability and its potential uses are enormous. Allard stated (personal communication): "For a good source of plant material, I would not go to the world collection of barley, but I would go to my populations."

Bulk populations are a good way of conserving genetic variability, accumulating genes, and obtaining a high level of general or horizontal resistance. I can see many uses in the Lesser Developed Countries, where research money, space and expertise are often scarce. With a minimum of effort, stable population systems can be established. If well managed, they will move towards greater adaptation in each specific environment and have great potential for future improvement of crop plants. Specific tests and selection procedures can be conducted in samples from populations to satisfy immediate needs, while the populations will keep evolving with all their genetic potential intact.

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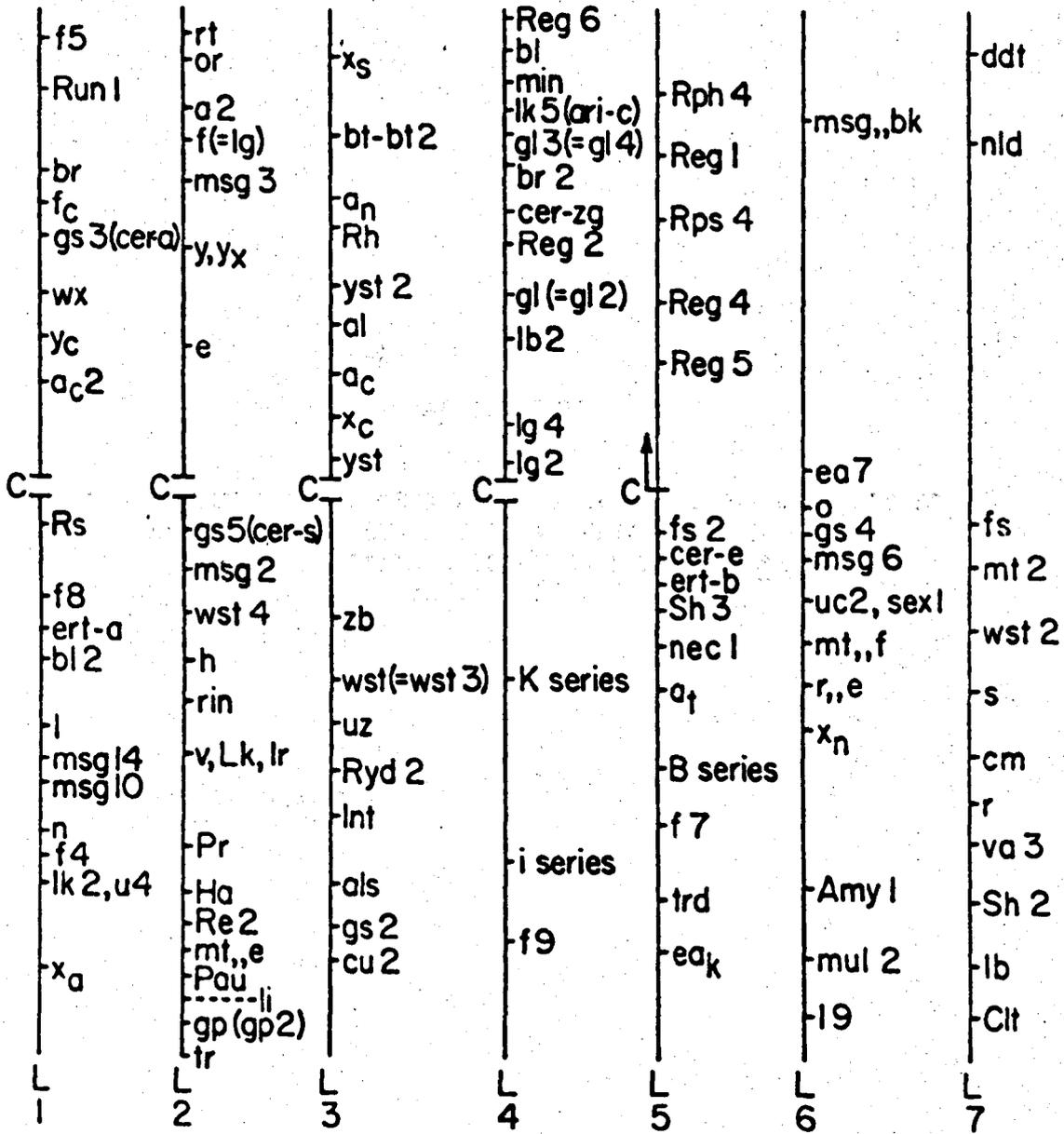
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APPENDICES

APPENDIX I

LINKAGE MAPS OF BARLEY. Tsuchiya (81)



APPENDIX II

THE BARLEY CHROMOSOME 5 LINKAGE MAP WITH THE BEST FIT TO
ALL AVAILABLE LINKAGE DATA. THE POSITION OF THE
CENTROMERE IS PROBABLY SLIGHTLY ABOVE fs2

Jensen (32)

Locus	
name	position (cM) ^a
Ml-at	107.8 ± 4.5
Pa4	84.4 ± 3.7
HrdE	74.6 ± 3.7
HrdD	74.4 ± 3.7
HrdC	74.1 ± 3.2
Hor2	71.7 ± 3.7
Ml-a	69.9 ± 3.6
Hor1	65.0 ± 3.6
Yr4	63.7 ± 3.8
Ml-k	62.2 ± 3.5
ml-d	50.6 ± 3.8
Lys4d	49.7 ± 8.7
Ml-nn	46.1 ± 4.0
Ml-p	32.7 ± 3.9
fs2	17.2 ± 4.4
cer-zi	16.0 ± 3.0
cer-e	14.8 ± 4.3
ert-b	14.6 ± 3.2
necl	0
at	-15.0 ± 3.2
wst 5	-38.0 ± 3.2
B	-59.6 ± 3.2
f7	-69.3 ± 3.3
trd	-74.5 ± 3.3
ea-k	-76.8 ± 3.4

^aCM = centimorgans (31).

APPENDIX III

SUMMARY OF EVIDENCE ON THE NATURE OF SELECTIVE
FORCES IN COMPOSITE-CROSSES OF BARLEY
Jain and Qualset (29)

Locus or trait	Mode of Selection	Evidence or kind of experimental test
B (pericarp color) V (2-row, 6-row) S (rhachilla hairiness) G (lemma dentation)	Directional selection for alleles b, v, s, and g	Genotypic frequency changes with advancing generations
R (awn barbing)	Heterozygote advantage in mean and stability of seed output; neighborhood effect in competition	Higher survival rate of Rr class, relatively higher in low frequency
Bl (aleurone color)	Heterozygote advantage in seed output; distorted segregation ratios favoring rarer allele	Higher net survival of heterozygotes and evidence for a linked gametophytic factor
Ms (male sterility)	Lower fecundity of <u>msms</u> but partially compensated through increased rates of outbreeding and heterozygote output	Delayed loss of male sterile from populations; association with heterozygotes at other loci, e.g., R, Bl
Days to heading Seed size Spike length Spike density	Stabilizing selection	Very small changes in population means but reduction in variances due to the elimination of extreme classes
Seed yield per plant or per pot	Directional selection	Slow and steady increase after initial phase of no change
Overall phenotypic and genetic variability	Varying rates of decrease in different populations due to a complex array of selective forces	

