Conservation of Scald Resistance in Barley Composite Cross Populations

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ABSTRACT

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The barley-*Rhynchosporium secalis* host-parasite system was used as a model to evaluate the potential of barley (*Hordeum vulgare*) composite cross populations for conservation of disease resistance alleles. Four isolates of *R. secalis* were used to monitor the frequencies of specific scald resistances through early, intermediate, and late generations of three composite cross populations (CC II, CC V, 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 generation F_{47}. Trends in frequencies of resistance are discussed in relation to the conservation of genes for disease resistance, and the degree of disease control provided by genetically diverse populations.

Additional key words: plant breeding.

Disease resistance as a method of plant disease control frequently has featured single genes conditioning vertical resistance (35) and often has resulted in "boom and bust" cycles when variable pathogens are involved (5, 7, 10, 19, 22, 26, 28, 30, 35). Races of a pathogen able to overcome new genes for resistance in the host often increase in frequency in the pathogen population and ultimately render the host resistance ineffective. A different gene for resistance is then incorporated and the cycle is repeated.

Other strategies for disease control through host resistance propose the use of mechanical mixtures of several different sources of resistance in multilines or synthetics, or the pyramiding of several genes for resistance in a single cultivar (5, 7, 17, 19, 20). It has been postulated that these strategies delay the "breakdown" of resistance: (i) by presenting a more formidable obstacle than vertically resistant cultivars for the variable pathogen to overcome and (ii) by delaying epidemic development. Nevertheless, races able to overcome the host defenses may arise and increase proportionally in the pathogen population and the search for new resistance must again be launched.

Rhynchosporium secalis (Oud.) Davis, causal agent of scald of barley, is highly variable in pathogenicity. Seventy-five races have been identified from a sample of the fungus population in California on the basis of differential reactions by 14 barley cultivars representing a wide range of genes for resistance to *R. secalis* (14). This complex racial population exists on commercially grown barley in California and, because these barleys lack known effective race-specific resistance, races with excess pathogenicity presumably have no advantage or disadvantage in the fungus population (20, 35). An early attempt to use vertical resistance resulted in only short-term control of scald disease; Atlas 46, which was released as resistant to California races of *R. secalis* in 1947, was susceptible throughout its range by 1956 (13). A population of *R. secalis,* made up by mixing four races in equal frequencies, contained 18 races following two successive disease cycles on a susceptible host in the greenhouse (15). This demonstrates that *R. secalis* is capable of adapting to changes in host resistance and it suggests that the gene pool of the natural population of *R. secalis* in California probably is very large respecting genetic variability for pathogenicity.

Long-term control of diseases caused by variable pathogens such as *R. secalis* through the use of host resistance depends on strategies that provide the flexibility needed to adapt to shifts in pathogen populations. Prior to the man-made imbalances that characterize modern intensive agriculture, host and pathogen existed in a state of fluctuating balance and interacted in such a way that disease, although present, rarely resulted in catastrophic crop losses (7, 8, 10, 11, 17). Because composite cross populations are managed to allow natural interactions to take place between host and pathogen, it is expected that alleles governing disease resistance will reach frequencies determined by natural selection (29, 31, 32, 34, 36). Thus, if variable forms of races of a pathogen are present, the corresponding resistant or susceptible members of the host population will increase or decrease in frequency depending on the relative selection pressures exerted by the respective races. It also is expected that the racial make-up of the fungus population will be affected by changes in the frequencies of specific resistant genotypes in the host population, again depending on their respective selective advantages. The collective result of these interactions might be satisfactory disease control.

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Barley composite cross populations and races of *R. secalis* are available to test the above theory. Barley populations synthesized as early as 1929 have been allowed to reproduce by their natural mating systems in Davis, California, without conscious selection (12, 32). Genes for scald resistance carried by the parents of these populations can be identified through the use of specific races of *R. secalis* (14), and their frequencies can be monitored from generation to generation in each population.

This paper reports results obtained using isolates of four races of *R. secalis* to monitor the frequencies of the corresponding specific resistances in early, intermediate, and late generations of three barley composite cross populations and discusses the value of composites in conserving genes for resistance and in providing an alternative strategy for disease control.

MATERIALS AND METHODS

The barley populations used for these studies were three composite crosses, Composite Cross II (CC II), Composite Cross V (CC V), and Composite Cross XXI (CC XXI). Since its synthesis (CC II in 1929, CC V in 1941, and CC XXI in 1959) each composite population has been grown in large plots in Davis, California, without conscious selection imposed by man. Each population has been exposed to a disease pressure which varies from year to year with environmental conditions and an adaptable *R. secalis* population which was not fully characterized until 1973 (14). Random seed samples of early, intermediate, and late generations of each composite population were germinated in the greenhouse and the resulting 2-wk-old seedlings were inoculated with each of four selected isolates of *R. secalis* to determine the frequencies of specific resistances in each sequence of generations tested.

Composite Cross II was synthesized in 1929 from 28 cultivars representing the major barley-growing regions of the world (12). The population was initiated by pooling equal amounts of F_1 hybrid seed from the 378 possible intercrosses among the parents and it has been propagated in large plots in Davis, California, each year under normal agricultural conditions without conscious selection (12, 32). The F_7, F_{15}, F_{25}, and F_{47} generations were used in greenhouse tests as respresentatives of early, intermediate, and late generations.

Composite Cross V differs from CC II in both parentage and method of synthesis. The population was synthesized from 30 parents, which like those of CC II, represent a wide sample of diversity in cultivated barley (29, 32, 33). The 30 parents, including 11 in common with CC II, were crossed in all possible pairs, the resulting F_1 hybrids again pair-crossed, and the cycle repeated until a single grand F_1 hybrid was obtained. The population was initiated from selfed seed produced by the grand hybrid in 1941. The population has since been propagated in Davis, California, in fashion parallel to CC II. The F_5, F_{12}, F_{23}, and F_{32} generations were tested in the present experiments.

Composite Cross XXI was produced from a much broader-based population than either CC II or CC V. It was synthesized by intercrossing 6,200 spring barley cultivars making use of a male-sterility gene (32, 34). The crosses were made in 1959, and the population has since been propagated like CC II and CC V at Davis, California. Representative test generations included the F_4, F_9, and F_{16}.

The fungus isolates were from a collection of California races of *R. secalis* maintained in the Department of Plant Pathology, University of California, Davis. One isolate of each of four races (races 40, 61, 72, and 74, deposited in the American Type Culture Collection under the accession numbers ATCC 34256, ATCC 34277, ATCC 34288, and ATCC 34290, respectively) was selected for use in the present studies. The basis of selection was the collective ability of the isolates to reveal distinct patterns of resistance in Composite Crosses II and V due to the presence of Atlas and Trebi, the only cultivars among the parents in which specific genes for resistance had been designated (14). Although additional sources of resistance among the parents to these isolates were identified, four patterns of resistance were still distinguishable.

The frequency of plants resistant to each isolate in each test generation was determined in greenhouse experiments. Standardized spore suspensions (2×10^5 spores/ml) of each isolate were prepared and inoculated singly onto samples of about 250 seedlings per generation in a controlled-environment chamber. Numbers of individuals inoculated per isolate-generation are given in Tables 2, 3, and 4. Inoculation and incubation methodologies are described elsewhere (14). Seedlings were grown in UC-Mix (18) in metal flats and inoculated at the one and one-half to three-leaf stage. Three flats (replicates), each containing 84 seedlings, were grown for each isolate-generation combination. After a 2-wk incubation period, each seedling was rated for scald reaction on a scale of 0-4; ratings of 0, 1, and 2 were grouped as resistant reactions and ratings of 3 and 4 were grouped as susceptible reactions as previously described (14). Frequencies of resistant plants were calculated for each isolate-generation combination; several of the combinations were repeated with additional population samples to confirm results. Analyses of variance were performed on angularly transformed frequency data to determine the statistical significance of observed differences in frequencies of plants resistant to each isolate within the generation sequence of each population.

RESULTS

Tests of the parents of CC II and CC V revealed that at least one parent of each population was resistant to each isolate of *R. secalis* (Table 1). In CC II, six of the parents were resistant to ATCC 34256, five were resistant to ATCC 34277, one was resistant to ATCC 34288, and three were resistant to ATCC 34290. In CC V five of the parents were resistant to ATCC 34256, seven were resistant to ATCC 34277, one was resistant to ATCC 34288, and five were resistant to ATCC 34290.

Tests of the populations themselves show that, although the frequency of resistant plants changed, plants resistant to each isolate remained in the population until the latest generation of each composite (Tables 2, 3, and 4). In CC V (Table 3) the frequencies of resistance to ATCC 34277, and ATCC 34288 did not change

significantly from generation F_5 to generation F_{32}. The frequencies of resistance to ATCC 34256 and ATCC 34290 dropped significantly ($P = 0.05$) between the early and intermediate generations, and leveled off at .12 for ATCC 34256 and at .04 for ATCC 34290 by generation F_{32}.

In the relatively short generation (F_4-F_{16}) sequence of the CC XXI population, there were only minor fluctuations in the frequencies of resistance to ATCC 34256, ATCC 34288, and ATCC 34290 (Table 4). The frequency of plants resistant to ATCC 34277 increased steadily, however, and the frequency was significantly greater ($P = 0.05$) in generation F_{16} (.30) than it was in generation F_4 (.13).

In CC II (Table 2), resistance to ATCC 34288 was maintained at a very low level, as was the case in CC V.

TABLE 1. Reaction of the parents of Composite Crosses II and V to four isolates of *Rhynchosporium secalis*

		Isolate[a]			
		34256	34277	34288	34290
Parent	C. I. No.[b]	40	61	72	74
Abate (V)	3920-1	S(4)	S(4)	S(4)	S(4)
Afghan I (V)	4166	S(3-4)	S(4)	S(4)	S(3-4)
Afghan II (V)	6366	S(4)	S(4)	S(4)	S(4)
Algerian (II, V)	1179	S(4)	S(4)	S(4)	S(3-4)
Alpha (II)	959	S(4)	S(4)	S(4)	S(3-4)
Arequipa (II, V)	1256	S(4)	S(4)	S(4)	R(2)
Atlas (II, V)	4118	S(4)	R(2)	R(1-2)	S(4)
Baker (V)	975	S(4)	S(4)	S(4)	S(4)
Black Algerian (V)	708	S(4)	S(4)	S(4)	S(4)
Bonfarik (V)	3393-1	S(4)	S(4)	S(4)	S(4)
Cal. Mariout (II)	1455	S(4)	S(4)	S(4)	S(3-4)
Club Mariout (II, V)	261	S(4)	S(4)	S(4)	S(4)
Coaston (V)	6626	S(4)	S(4)	S(4)	R(2)
Everest (II)	4105	S(4)	S(4)	S(4)	S(4)
Ezond (V)	6265	R[c](0-2)	R(0)	S(4)	R(0-2)
Flynn (II, V)	1311	S(4)	S(4)	S(4)	S(3)
Glabron (II)	4577	R(0-1)	R(2)	S(4)	R(0-2)
Golden Pheasant (II)	2488	S(4)	S(4)	S(4)	S(4)
Good Delta (II)	3801	S(3)	S(4)	S(4)	S(4)
Goodwill (V)	6083	S(4)	S(4)	S(4)	S(4)
Hannchen (II)	531	S(4)	S(4)	S(4)	S(4)
Han River (II, V)	206	R(0-2)	R(1-2)	S(4)	S(3-4)
Horn (II)	926	S(4)	S(4)	S(4)	S(4)
Lion (II, V)	2591	S(4)	S(4)	S(4)	S(4)
Lioness (V)	4019	S(4)	S(4)	S(4)	S(4)
Lyallpur (II)	3395	R(0-2)	S(4)	S(4)	S(4)
Maison Caree (II, V)	3388	R(0-2)	R(0-2)	S(4)	R(0-2)
Manchuria (II)	2947	S(3)	S(4)	S(3-4)	S(3-4)
Meloy (II)	1176	S(4)	S(4)	S(4)	S(4)
Minia (II, V)	3556	S(4)	S(4)	S(4)	S(4)
Multan (II)	3401	S(3-4)	S(4)	S(4)	S(4)
New ZZ (V)	6299	S(4)	S(3-4)	S(4)	S(4)
Oderbrucker (II)	4666	R(2)	S(4)	S(4)	S(3-4)
Old ZZ (V)	6298	S(4)	R(2)	S(3-4)	S(4)
Orel (II)	351	S(4)	S(4)	S(4)	S(4)
Pamella Blue (II)	3609	S(4)	S(4)	S(4)	S(4)
Pannier (V)	1330	S(4)	S(4)	S(3-4)	S(4)
Parla (V)	3513-1	S(4)	S(4)	S(4)	S(4)
Peatland (V)	5267	S(3-4)	S(4)	S(4)	S(3-4)
Rikote (V)	5888	S(4)	S(4)	S(4)	S(4)
Sandrel (II, V)	937	S(4)	S(4)	S(4)	S(4)
Stavropol (V)	2103	S(4)	S(4)	S(4)	S(4)
Trebi (II, V)	936	R(0-1)	R(1)	S(4)	S(3-4)
Vaughn (V)	1367	S(4)	S(4)	S(3-4)	S(4)
Velvon (V)	6109	R(0)	R(0)	S(4)	R(0)
White Smyrna (II)	910	S(3-4)	S(4)	S(4)	S(3-4)
Wisconsin Winter (II)	519	S(3-4)	S(4)	S(4)	S(4)
CC II, number resistant parents		6	5	1	3
CC V, number resistant parents		5	7	1	5

[a]American Type Culture Collection accession numbers for isolates or races 40, 61, 72, and 74, respectively.
[b]U.S. Department of Agriculture Cereal Inventory numbers.
[c]Symbols: R = resistant; 0, 1, or 2 seedling reaction in greenhouse tests.

However, the frequencies of plants resistant to the three other isolates increased until they reached very high levels by generation 47: the increases were from .18 to .85, .23 to .78, and .28 to .92 for ATCC 34256, ATCC 34277, and ATCC 34290, respectively. In each case the largest increase occurred from generation 25 to generation 47.

TABLE 2. Frequencies of resistance in barley Composite Cross II populations to four isolates of *Rhynchosporium secalis*

Isolate[w]	Generation	Disease rating					N[x]	R[y]
		0	1	2	3	4		
34256								
40	F(7)	2	2	8	8	228	248	.05 a[z]
	F(15)	2	2	16	7	207	234	.08 b
	F(25)	6	10	26	7	187	236	.18 c
	F(47)	80	46	68	9	26	229	.85 d
34277								
61	F(7)	1	3	21	3	207	235	.11 a
	F(15)	1	10	18	6	201	236	.12 a
	F(25)	13	12	32	8	180	245	.23 a
	F(47)	55	37	83	8	41	224	.78 b
34288								
72	F(7)	0	1	4	5	236	246	.02 a
	F(15)	0	0	1	1	234	236	<.01 a
	F(25)	0	0	1	6	218	225	<.01 a
	F(47)	0	0	9	17	210	236	.04 a
34290								
74	F(7)	1	16	25	10	197	249	.17 a
	F(15)	8	10	16	13	195	242	.14 a
	F(25)	27	32	7	16	153	235	.28 b
	F(47)	137	76	5	1	17	236	.92 c

[w]American Type Culture Collection accession numbers for isolates of race 40, 61, 72, and 74, respectively.
[x]Number of individuals inoculated per isolate-generation.
[y]Frequency of resistance = sum of ratings of 0, 1, and 2 divided by N.
[z]Means (after arcsine transformation) 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.

TABLE 3. Frequencies of resistance in barley Composite Cross V populations to four isolates of *Rhynchosporium secalis*

Isolate[w]	Generation	Disease rating					N[x]	R[y]
		0	1	2	3	4		
34256	F(5)	25	20	15	9	170	239	.25 a[z]
40	F(12)	16	10	18	11	178	233	.19 a
	F(23)	2	5	18	15	197	237	.10 b
	F(32)	3	3	23	21	191	241	.12 b
34277	F(5)	8	13	13	8	199	241	.14 a
61	F(12)	6	20	11	8	189	234	.16 a
	F(23)	2	9	12	11	207	241	.10 a
	F(32)	2	12	19	10	192	235	.14 a
34288	F(5)	0	6	5	3	225	239	.05 a
72	F(12)	0	6	10	7	211	234	.07 a
	F(23)	0	7	3	1	145	156	.06 a
	F(32)	0	4	4	5	221	234	.03 a
34290	F(5)	8	19	12	8	199	246	.16 a
74	F(12)	3	18	11	5	196	233	.14 a
	F(23)	0	4	4	0	235	243	.03 b
	F(32)	1	7	2	3	222	235	.04 b

[w]American Type Culture Collection accession numbers for isolates of races 40, 61, 72, and 74, respectively.
[x]Number of individuals inoculated per isolate-generation.
[y]Frequency of resistance = sum of ratings of 0, 1, and 2 divided by N.
[z]Means (after arcsine transformation) 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.

Additionally, there were significant ($P = 0.05$) increases in the frequency of plants resistant to ATCC 34290 between generations F_{15} and F_{25}, and to ATCC 34256 between all generations tested. Tests with ATCC 34256, ATCC 34277, and ATCC 34290 on additional samples from generations F_7, F_{15}, F_{25}, and F_{47} gave nearly identical results.

DISCUSSION

A number of authors (1, 3, 4, 11, 26, 31, 34) have presented evidence that composite cross populations provide an effective method of conserving genetic variability. In the present study it was found that resistance to four isolates of *R. secalis* has persisted through the latest generation examined in each of three composite cross populations (F_{47} in CC II, F_{32} in CC V, and F_{16} in CC XXI). Thus, the usefulness of composite crosses for the conservation of genetic variability also extends to genes governing disease resistance. In this connection, it should be noted that the adaptation and the yield of composite crosses has been found to increase as the populations have evolved (26, 29, 32, 33, 34). Therefore, it is expected that disease resistant selections taken from advanced generations of composite crosses would be well adapted to the environment in which the composite cross has been maintained and hence that they would make desirable parents in conventional plant breeding programs.

The dramatic increases in the frequencies of plants resistant to three of the isolates of *R. secalis* that were observed in CC II stand in marked contrast to the small changes that occurred for the fourth isolate in CC II and for all isolates in CC V and CC XXI. It is unlikely, for two reasons, that the large increases that occurred in CC II resulted solely from selection pressures imposed by scald disease. First, the development of scald disease depends on environmental conditions (9, 14, 21, 25) and in many years conditions are unfavorable for the development of the disease in California (24). In the years when scald is virtually nonexistent it is difficult to imagine that resistance would confer selective advantage on any member of the host population. Thus, in many years selection pressure favoring resistant individuals must be too low to cause changes in the frequency of genes for resistance. Second, the race composition of this adaptable fungus may shift from year to year (13, 15); therefore, it is unlikely that resistance to any given race is equally advantageous in each year that scald is severe. It is difficult to explain the changes in frequency of resistant plants which were observed in CC II to selection for specific resistance because such selection is expected to produce differing rather than nearly identical trends for races with such divergent patterns of pathogenicity as races 40, 61, and 74.

A possible cause for the rapid changes in specific resistances that occurred in CC II is that the alleles involved were associated with traits that confer selective advantage. Studies of the composite cross utilizing enzyme loci as markers have revealed that these populations rapidly develop highly organized population structures featuring coadapted gene complexes involving striking nonrandom associations of alleles at different genetic loci (2, 6, 16, 36). It is possible that alleles governing specific resistance were associated with such favored coadapted complexes in certain of the parents of CC II and that the resistance alleles were pulled along as selection caused the complexes to increase in frequency. This possibility is being tested by scoring progeny of random individuals, taken from the composite cross populations, for disease reaction, morphological polymorphisms, enzyme polymorphisms, and various quantitative characters simultaneously to determine whether such associations exist.

Emphasis to this point has been on specific resistance but interactions between host and parasite in composite cross populations might also favor resistance alleles in

TABLE 4. Frequencies of resistance in barley Composite Cross XXI populations to four isolates of *Rhynchosporium secalis*

Isolate[w]	Generation	Disease rating						
		0	1	2	3	4	N[x]	R[y]
34256	F(4)	11	3	5	1	222	242	.08 a[z]
40	F(9)	25	4	10	2	205	246	.16 a
	F(16)	6	4	64	4	219	239	.07 a
34277	F(4)	10	18	4	6	205	243	.13 a
61	F(9)	14	23	13	12	175	237	.21 ab
	F(16)	20	38	13	5	163	239	.30 b
34288	F(4)	0	16	16	3	208	243	.13 a
72	F(9)	4	18	18	6	195	241	.17 a
	F(16)	4	10	26	9	191	240	.17 a
34290	F(4)	10	14	1	7	214	246	.10 a
74	F(9)	13	19	4	11	196	243	.15 b
	F(16)	10	13	3	3	210	239	.11 a

[w] American Type Culture Collection accession numbers for isolates of races 40, 61, 72, and 74, respectively.
[x] Number of individuals inoculated per isolate-generation.
[y] Frequency of resistance = sum of ratings of 0, 1, and 2 divided by N.
[z] Means (after arcsine transformation) 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.

polygenic systems, leading to improvement in horizontal resistance (23, 26, 27). We have observed later onset of scald symptoms and subsequent slower disease development on seedlings of the later generations of CC II, CC V, and CC XXI in the greenhouse suggesting that this phenomenon may be occurring in these composite cross populations.

Observations of the composite cross populations over many years suggest that these populations, especially the later generations, are less affected by scald disease than commercial cultivars. Studies are now underway to determine the yielding ability of the barley populations under different levels of scald infection and the extent of year-to-year fluctuations in frequencies of resistance. Results of this work should be useful for determining the level of resistance required in populations to provide acceptable disease control under conditions of varying pathogen pressure. In addition, these studies should provide information concerning the value of genetically diverse populations for adequate disease control.

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