Geographical Distribution and Associations Between Resistance to Four Races of *Rhynchosporium secalis*

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ABSTRACT

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Data from an assay of a random sample of 350 accessions of barley from the USDA world collection for reaction to four physiological races (races 40, 61, 72, and 74) of *Rhynchosporium secalis* were analyzed using a disease index, Shannon's information statistic, and product-moment correlation. Accessions from different geographical areas differ in degree of resistance to the four races individually and in levels of diversity for resistance to the four races jointly. The races studied differ in aggressiveness, which was negatively associated with racial complexity. Race 40 (the most simple race) was the most aggressive race and race 74 (the most complex race) was the least aggressive. The proportions of the total variability accounted for by various components of the hierarchical geographical structure are: differences among different regions 4%, differences between countries within regions 6%, differences between accessions within countries 37%, and heterogeneity within accessions 53%; the factors responsible for the large within-accession diversity are unknown. Resistance to races 40, 61, and 74 was positively associated, but resistance to race 72 was independent of the other three races.

Scald, a serious disease of barley *Hordeum vulgare* L., is caused by *Rhynchosporium secalis* (Oud.) Davis. Attempts to control scald have been primarily through the breeding and cultivation of resistant cultivars. Resistant varieties, however, have given only temporary control primarily due to breakdown of resistance associated with shifts in the racial composition of the pathogen. Jackson and Webster (4) found that the racial composition of *R. secalis* can be complex, with at least 75 different physiological races existing in the Sacramento and San Joaquin valleys of California. Webster et al (12) evaluated more than 18,000 entries from the USDA barley collection by inoculating plants with a mixture of conidia of five races of *R. secalis*. Only nine entries from six countries showed no symptoms; only 274 entries, including representatives from three species of *Hordeum*, showed high levels of resistance. Thus, most barley accessions are susceptible to a complex population of *R. secalis*.

Workers in several countries have studied variability in pathogenicity of *R. secalis* and corresponding genetic variability for resistance in barley (1,3,4,10,12). However, information concerning geographical structure of genetic variability in both the host and the pathogen population is lacking. Relationships between races and disease levels have not been investigated on a large scale in world barley collections. In this study, genetic variability in resistance to four races of *R. secalis* was investigated in a random sample of 350 accessions from the world barley collection. The purpose was to assess geographical patterns of disease resistance and to characterize the distribution and associations of genetic variability quantitatively with respect to resistance to the four selected physiological races of *R. secalis*.

MATERIALS AND METHODS

The 350 accessions studied were chosen randomly from the world barley collection maintained by the USDA in Beltsville, MD. The 40 countries represented in the sample were grouped geographically into 12 regions, following (with minor modifications) the grouping of Kahler and Allard (6) (Table 1). The accessions are land races collected in small samples from various barley growing areas of the world (7). When the seed supply of a particular entry becomes scarce, the stock is replenished by growing the seeds in a small plot, and the seeds harvested from such plots are mixed and stored as seed sources (6). As expected, large amounts of genetic variability are lost in the maintenance of the seed stocks, because of genetic drift and an extremely high degree of self-fertilization (>99%). Studies on the same 350 accessions (14) for eight allozyme loci and six morphological markers showed that the entries were genetically highly homogeneous with respect to these marker loci: less than 9% of the worldwide allozyme polymorphism and less than 4% of diversity in morphological markers were due to within-accession heterogeneity.

Resistance reactions to *R. secalis* races 40, 61, 72, and 74 (ATCC34256, ATCC34277, ATCC34288, and ATCC34290, respectively) were determined for each accession. These races were chosen because, in combination, they are capable of overcoming all reported resistance genes in barley (4).

Inoculum was produced by seeding potato-dextrose agar plates with a spore suspension, incubating the plates at 15 C for 14 days, and harvesting the conidia in tap water. Inoculum concentration was adjusted to 2.5×10^5 conidia per milliliter. The inoculation procedure of Jackson and Webster (4) was closely followed. Many studies showed that results produced by this inoculation method were highly repeatable (3–5,8,13).

Fifteen seeds of each accession were planted in UC soil mix C-2 in metal flats and seedlings allowed to grow in a greenhouse for 2 wk before inoculation. Each flat was inoculated with 50 ml of spore suspension, transferred to a growth chamber in which the humidity was at 100%, and returned to the greenhouse after 48 hr. A random sample of 10 seedlings of each accession was scored individually for disease 2 wk later. Scoring was based on a 0–4 grading following Jackson and Webster (4): 0 = no visible symptoms; 1 = very small lesions confined to leaf margins; 2 = small lesions not confined to leaf margins; 3 = large coalescing lesions involving a minority of the leaf area; and 4 = total collapse of the leaf.

In previous studies of the inheritance of resistance in barley and variability in *R. secalis* (1,4), the five categories (0–4) have been combined into two categories, resistant (0–2) and susceptible (3–4), to identify major genes for the disease reaction. Such consolidation of classes does not allow assessment of variation within categories *R* and *S* due to additional unknown genes for resistance to races 40,

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61, 72, and 74 and/or minor genes or other factors affecting virulence that may be present in barley accessions. Accordingly, a quantitative measurement of disease index (DI) was devised that recovers information from disease scores 0, 1, 2, 3, and 4 as follows:

$$DI = \sum_j jf_j / 4 \sum_j f_j$$

where f_j = number of individuals in the jth category. The variance of the disease index, $V(DI)$, is given by

$$V(DI) = \sum_j f_j(j - \sum_j jf_j / \sum_j f_j)^2 / 16(\sum_j f_j)(\sum_j f_j - 1).$$

DI can take value from 0 (if every individual in an entry scores 0) to 1 (if every individual scores 4). An approximate test criterion could be constructed to compare differences between DI values of different samples. To be at the conservative side, we used the

TABLE 1. Disease indices (DI) and their standard errors (S.E.) derived from inoculation with four races of *Rhynchosporium secalis* on barleys from different geographical areas

		Race 40		Race 61		Race 72		Race74	
Location	Accessions	DI	S.E.	DI	S.E.	DI	S.E.	DI	S.E.
North West Europe	65								
Finland	4	0.668	0.063	0.475	0.059	0.656	0.057	0.469	0.555
Czechoslovakia	1	0.475	0.069	0.950	0.033	0.875	0.042	0.225	0.069
Switzerland	1	0.475	0.102	0.275	0.058	0.775	0.025	0.025	0.025
Sweden	11	0.675	0.034	0.489	0.033	0.484	0.033	0.395	0.034
Denmark	7	0.704	0.046	0.596	0.043	0.504	0.034	0.604	0.044
England	12	0.827	0.022	0.510	0.033	0.560	0.031	0.433	0.303
Scotland	1	1.000	0.000	0.875	0.067	0.900	0.055	0.750	0.099
Ireland	5	0.790	0.044	0.740	0.043	0.370	0.049	0.760	0.037
Poland	12	0.452	0.037	0.404	0.034	0.352	0.025	0.198	0.022
France	10	0.790	0.031	0.710	0.037	0.717	0.030	0.707	0.040
Austria	1	0.675	0.123	0.550	0.128	0.775	0.058	0.475	0.120
Region		0.690	0.014	0.552	0.015	0.535	0.013	0.467	0.015
S. Europe	20								
Spain	4	0.569	0.065	0.575	0.070	0.456	0.057	0.419	0.054
Italy	8	0.847	0.035	0.747	0.042	0.716	0.040	0.625	0.045
Romania	3	0.392	0.070	0.333	0.085	0.525	0.066	0.225	0.051
Greece	3	0.875	0.041	0.750	0.046	0.857	0.035	0.692	0.063
Region		0.714	0.029	0.640	0.031	0.653	0.027	0.524	0.029
USSR	20	0.806	0.020	0.587	0.027	0.795	0.018	0.364	0.026
South West Asia	29								
Cyprus	3	0.642	0.084	0.742	0.067	0.783	0.044	0.617	0.080
Turkey	13	0.527	0.037	0.513	0.037	0.548	0.029	0.421	0.036
Iraq	10	0.862	0.025	0.732	0.030	0.625	0.036	0.310	0.035
Israel	3	0.533	0.067	0.583	0.075	0.642	0.054	0.350	0.044
Region		0.655	0.023	0.620	0.023	0.609	0.020	0.396	0.023
Middle South Asia	48								
Iran	15	0.723	0.028	0.558	0.032	0.665	0.029	0.487	0.029
Afghanistan	14	0.834	0.026	0.548	0.033	0.895	0.017	0.316	0.029
India	17	0.854	0.020	0.656	0.028	0.794	0.018	0.434	0.032
Nepal	2	0.950	0.029	0.287	0.055	0.612	0.056	0.737	0.061
Region		0.811	0.014	0.579	0.018	0.775	0.013	0.429	0.017
East Asia	53								
China	23	0.845	0.020	0.626	0.026	0.852	0.017	0.656	0.024
Korea	15	0.912	0.016	0.858	0.016	0.832	0.021	0.600	0.031
Japan	15	0.730	0.029	0.563	0.032	0.635	0.031	0.648	0.031
Region		0.831	0.013	0.674	0.016	0.785	0.013	0.638	0.016
North Africa	36								
Egypt	18	0.817	0.024	0.537	0.028	0.675	0.021	0.457	0.028
Ethiopia	12	0.479	0.040	0.294	0.035	0.481	0.035	0.333	0.032
Algeria	5	0.455	0.059	0.305	0.057	0.755	0.034	0.320	0.048
Morocco	1	0.825	0.053	0.975	0.025	1.000	0.000	0.350	0.100
Region	0.654	0.022	0.436	0.021	0.631	0.018	0.394	0.019	
South Africa	7	0.921	0.019	0.654	0.044	0.593	0.044	0.729	0.039
Australia	14	0.850	0.021	0.680	0.028	0.664	0.025	0.273	0.025
Central America	14								
Mexico	8	0.875	0.028	0.728	0.041	0.562	0.040	0.509	0.042
Guatemala	6	0.954	0.013	0.712	0.039	0.362	0.041	0.733	0.035
Region		0.909	0.017	0.721	0.029	0.477	0.030	0.605	0.030
South America	19								
Peru	1	0.900	0.041	0.800	0.062	0.050	0.050	0.050	0.033
Venezuela	6	0.958	0.016	0.829	0.035	0.912	0.019	0.642	0.048
Chile	3	0.783	0.049	0.417	0.070	0.575	0.079	0.367	0.084
Argentina	9	0.508	0.043	0.400	0.044	0.694	0.035	0.192	0.029
Region		0.714	0.027	0.559	0.030	0.710	0.026	0.354	0.028
United States	27	0.597	0.028	0.501	0.026	0.470	0.022	0.267	0.020
World	350	0.743	0.006	0.585	0.007	0.651	0.006	0.453	0.007

confidence intervals (CI) to evaluate statistical significance of differences between DI values. The DI values of the two samples were considered as being significantly different at the 0.05 probability level if the 95% CI's of the two DI's did not overlap.

The diversity of resistance among a group of plants to the *i*th race was evaluated by Shannon's information statistic (h_i) given by Bowman et al (2):

$$h_i = -\sum_j (f_{ij}/\sum_j f_{ij}) \ln(f_{ij}/\sum_j f_{ij}), \text{ and for all } j = 0, 1, 2, 3, \text{ and } 4,$$

where fij is the number of individuals observed in the jth category of race i. The diversity index of resistance of a group of plants to the four races as a whole was estimated by $H = \Sigma h_i/4$, for all $i = 1, 2, 3$, and 4.

An important property of this statistic is that the diversity measure of a large population can be partitioned into components associated with divergence between and diversity within subpopulations and it therefore allows assessment of the relative magnitude of each component.

RESULTS AND DISCUSSION

Distribution of scald resistance in geographical regions. Disease indices and their standard errors for the four races on accessions from various geographical areas, calculated using the above formulas, are given in Table 1. The numbers of accessions from six of the 12 regions (N. W. Europe, S. W. Asia, M. S. Asia, E. Asia, N. Africa, and United States) were close to or larger than 30. Consequently, detailed comparisons were made only among accessions from these six regions. We will describe the analysis in detail for race 40 only.

The disease index of race 40 on the 350 accessions is 0.743. The disease index of a region was calculated by pooling all the individuals from that region. Many of the regional differences were statistically significant as shown by the 95% of the confidence intervals (Fig. 1). Among the six regions with relatively large sample sizes, accessions from M. S. Asia and E. Asia were the most susceptible with DI values equal to 0.811 and 0.831, respectively, which were not different statistically. The DI values for the regions N. W. Europe, S. W. Asia, and N. Africa are 0.690, 0.655, and 0.654, respectively, which were not significantly different from each other but were different from the DI values of M. S. Asian and E. Asian accessions at the 0.05 level. The DI of the U.S. accessions was the lowest (0.597). Although this DI did not differ statistically from the DI values of S. W. Asia and N. Africa accessions, it was nevertheless significantly lower than the DI's of the accessions from N. W. Europe, S. W. Asia, and E. Asia. Disease indices for individual countries may not be representative of the true values because the number of accessions sampled from many countries was small and detailed information about the geographical distribution and the amount of each accession grown in a country was not always available. Nevertheless, it is evident from Table 1 that variation in disease indices was large among different countries within regions, which may not be accounted for by sampling alone. For example, the DI of N. African accession from Egypt was 0.817 for race 40 (95% CI 0.708–0.865), whereas the DI of accession from Ethiopia was 0.479 (95% CI 0.400–0.558). Differences between disease indices for different accessions within countries were also frequently significant statistically. Table 2 gives an example: In Ethiopia accession CI 2325 had 0 disease index for race 40 but that of CI 9942 was 0.95.

Similar comparisons can be made by using the DI values for races 61, 72, and 74 (Table 1). Comparison of the disease indices for all four races showed that, among the six regions that justified detailed comparisons, the E. Asian barleys appeared to be the most susceptible and the barleys of the United States the least susceptible. Comparisons of DI values among countries across the regions indicated that disease indices appeared to be low for Polish and Ethiopian barleys (Tables 1 and 2). Some accessions had low DI values for all four races (Table 2), which suggested that these accessions may be useful as sources of scald resistance in barley breeding.

Differential reactions to the four races. The top line of Fig. 1 gives the 95% confidence intervals for DI values for each of the four races tested. The DI for race 40 was the largest (0.743, 95% CI 0.731–0.755), followed by race 72 with DI = 0.621 (95% CI 0.610–0.663), race 61 with DI = 0.585 (95% CI 0.572–0.598), and race 74 with DI = 0.453 (95% CI 0.440–0.466). None of the confidence limits overlapped, indicating that the differences among the DI's of races 40, 61, 72, and 74 were statistically significant. Among possible explanations were: that unknown genes that impart resistance to particular races are present in accessions from some areas, or that the specific isolates of the pathogen tested differ in aggressiveness, i.e., differ quantitatively in their ability to incite disease symptoms, as revealed by DI values calculated from disease scores 0, 1, 2, 3, and 4. If unknown genes for resistance were involved (explanation 1), it was expected that disease indices for a particular race would be low in some regions and that the pattern found in those regions would differ from the patterns of other regions, as well as for the world as a whole. If differential aggressiveness was involved (explanation 2), the patterns for different regions would be similar assuming genes for resistance were randomly sampled from different regions. Races of the pathogen differ in complexity: complex races are defined as ones that are capable of producing disease on a larger number of differential strains of the host than simple races of the same species, i.e., complex races possess more virulence genes than do simple races (13). The results of Jackson and Webster (4) showed that the order of racial complexity among these four races was: Race 74 > race 72 > race 61 > race 40. The severity of scald for the 350 accessions is negatively associated with complexity of the pathogen, and this trend held for 10 of the 12 regions (Table 1). The sample sizes were smallest for the remaining two regions (S. Africa 7, C. America 14), which might be responsible for the differences in the order of disease severity of the four races between these two regions and the other 10 regions. It therefore seemed unlikely that the variation in disease indices of these races is due to unknown resistance genes in the barley accessions of given regions and that the variation instead reflected differences in the aggressiveness of the races. The results of this study were thus consistent with the hypothesis (11) that selection decreases frequencies of "unnecessary" virulence genes and favors aggressive races when virulence genes are needed for reproduction of pathogen on the host.

In summary, the data showed that observed disease indices varied greatly from area to area for given races, indicating geographical differentiation of resistance, the races differed in aggressiveness on different barleys, and the differences were related to the "complexity" of the pathogen races tested.

Diversity of resistance to *R. secalis*. The diversity index of resistance to the *i*th race of the pathogen for each accession was estimated using Shannon's information statistic (h_i). Diversity indices averaged over resistance to the four test races (H) within accessions, within countries, and within regions, are given in Table 3. Comparisons were also only made among the six regions that had relatively large sample sizes.

Within-accession diversity. For a particular region, within-accession diversity is estimated as the average diversity over all the accessions from that region. Among the six regions, N.W. Europe had the highest within-accession diversity ($H_W = 0.866$), accessions from S. W. Asia, M. S. Asia, E. Asia, and the United States appeared to be intermediate (0.745 about equal to 0.785). and N. African barleys were low in within-accession diversity (H_W = 0.581).

Within-country diversity. Diversity among accessions within countries varied over a very wide range. We were unable to identify any pattern of within-country diversity, e.g., diversity was high within some large, geographically diverse countries such as the United States (1.477) but also high within some small geographically uniform countries such as Denmark (1.453). In contrast, diversity was relatively low in some large, geographically diverse countries such as China (1.209) and also low in Italy (1.193), a relatively small, geographically uniform country.

Within-region diversity. Within-region diversity indices varied from 1.287 (E. Asia) to 1.537 (N. W. Europe) among the six regions. N. Europe, S. W. Asia, N. Africa, and the United States had generally high diversity indices (> 1.400), whereas M. S. Asia had low values (< 1.360).

Allocation of diversity. The nature of the diversity statistic allows partition of the diversity into components that reflect genetic divergence among populations (genetic distance) as well as diversity within subpopulations. In the present case, diversity measures of the barley accessions, averaged over the four races tested, can be partitioned into measures of genetic distances among regions and diversity within regions. Diversity within regions can similarly be partitioned into measures of genetic distances among countries within regions and diversity within countries; the last can

TABLE 2. Disease indices and standard errors for reaction of four races of *Rhynchosporium secalis* with Ethiopian and Polish barley accessions

	Race 40		Race 61		Race 72		Race 74	
Accession	DI	S.E.	DI	S.E.	DI	S.E.	DI	S.E.
Ethiopia								
2223	0.775	0.087	0.000	0.000	0.950	0.033	0.000	0.000
2225	0.925	0.053	0.000	0.000	0.475	0.025	0.025	0.083
2226	0.025	0.025	0.000	0.000	0.000	0.000	0.000	0.000
2325	0.000	0.000	0.025	0.025	0.075	0.053	0.000	0.000
2377	0.100	0.041	0.075	0.053	0.700	0.050	0.125	0.067
2383	0.675	0.099	0.075	0.053	0.850	0.100	0.475	0.058
3920	0.075	0.053	0.275	0.087	0.450	0.117	0.625	0.085
3927	0.050	0.050	0.350	0.100	0.300	0.122	0.550	0.073
4326	0.375	0.107	0.850	0.067	0.975	0.025	0.075	0.075
9942	0.950	0.033	0.625	0.085	0.400	0.076	0.825	0.038
9943	0.875	0.056	0.375	0.130	0.200	0.082	0.725	0.095
14119	0.925	0.038	0.875	0.077	0.400	0.067	0.350	0.076
Country	0.479	0.048	0.294	0.035	0.481	0.035	0.333	0.032
Poland								
6280	0.425	0.112	0.100	0.041	0.275	0.102	0.025	0.025
6395	0.650	0.100	0.475	0.115	0.275	0.095	0.325	0.118
6397	0.200	0.082	0.425	0.099	0.050	0.033	0.225	0.079
6400	0.450	0.104	0.325	0.009	0.350	0.067	0.100	0.055
6401	1.000	0.000	1.000	0.000	0.525	0.102	0.325	0.053
6405	0.100	0.055	0.150	0.055	0.275	0.058	0.050	0.033
6410	0.000	0.000	0.000	0.000	0.275	0.079	0.000	0.000
6412	0.750	0.083	0.500	0.091	0.425	0.038	0.300	0.082
6424	0.225	0.069	0.400	0.067	0.525	0.108	0.225	0.058
6444	0.600	0.067	0.625	0.125	0.400	0.076	0.325	0.075
6448	1.000	0.000	0.775	0.045	0.625	0.056	0.475	0.079
6474	0.025	0.025	0.075	0.038	0.225	0.045	0.000	0.000
Country	0.452	0.037	0.404	0.034	0.352	0.025	0.198	0.023

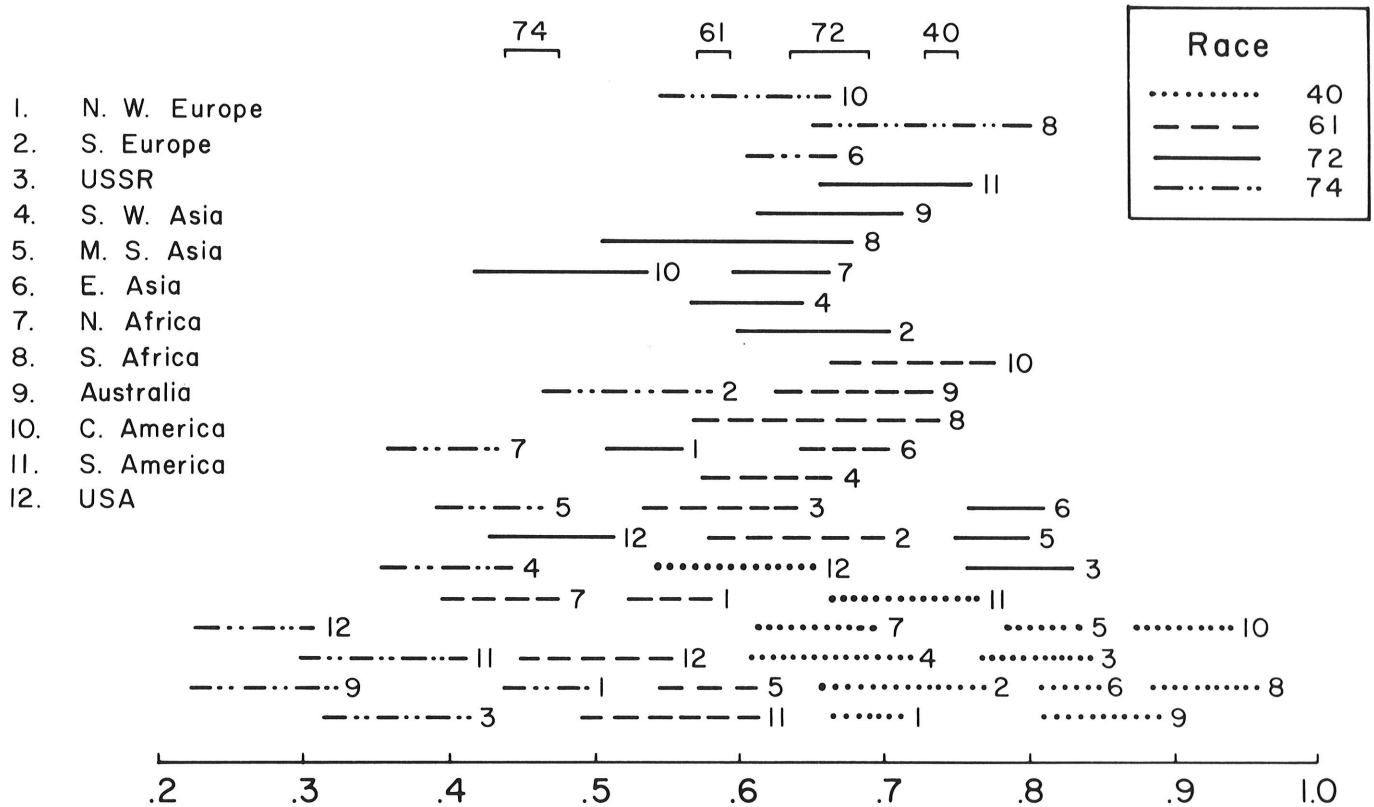

Fig. 1. Ninety-five percent confidence intervals for the disease indices of the infection of barley accessions from 12 geographical regions by four races of *Rhynchosporium secalis*.

in turn be partitioned into genetic distance between accessions and diversity within accessions.

The worldwide diversity (H = 1.462 from Table 3) was partitioned into relevant components (the bottom line of Table 4). Combining information provided by resistance to all four races, the estimated distance between regions (D_R) was 0.055, which accounted for less than 4% of the total variability. As noted previously, this component, although small, was a statistically significant part of the total diversity. The diversity value corresponding to divergence among countries within regions (D_C) was 0.082, which was about 6% of the total. This also represented a difference of statistical significance. These two components, which together accounted for about 10% of the total variability, can be ascribed to effects of macro-geographical differentiation. The estimated distance between accessions within countries (D_A) was 0.548, which was about 37.5% of the total variability. The component of diversity within accessions H_W = 0.777, was the largest, accounting for more than half (53.12%) of the total genetic diversity measured. The diversity within regions was also partitioned (Table 4). The diversity associated with the within-accession component was larger than 50% for all regions, the component of distance among accessions within countries ranges between 30 and 46%, and distance among countries within regions accounted for 15% or less of the total diversity.

Similar large amounts of within-accession diversity have been observed in earlier studies. Jackson et al (3) found that the late generations of an experimental population of barley (Composite Cross II, CCII) were equally and perhaps even more variable than early generations. Muona (8) reported that within-family diversity increased from early generations (e.g., F_8) to late generations (e.g., F_{45}) in CCII and she suggested that the population was in a transient state on the way to fixation or near fixation. It seems unlikely that subjectiveness in scoring and/or local environmental differences in the plots in which these experiments were conducted were responsible for the variability observed the late generations because plants of the same accessions (families in Muona's experiment) were grown side by side and scored at the same time. Also, most of the accessions studied in the present experiment were grown for long periods in the major barley-growing areas of the world, and it is expected that they would have reached equilibrium, or quasi-equilibrium, status in the large number of generations they had been grown before they were added to the USDA collection. Thus the large amount of within-accession variability observed may represent steady, rather than temporary, states for most and perhaps all, of the accessions studied. Additional studies have been initiated to identify the factors responsible for existence of such surprisingly large amounts of within-accession variability.

Associations between resistance to these four races. Arc-sine square-root transformed disease indices calculated for each accession were used as raw data in the calculation of pairwise product-moment correlations among the four races. The largest correlation was between race 40 and race 61 (r = 0.494 with 95% confidence interval 0.411–0.569), followed by that between race 61 and race 74 (r = 0.465, 95% CI 0.379–0.543) and that between race 40 and race 74 (r = 0.436, 95% CI 0.347–0.520) (Table 5). Thus about 20–25% of the variability in any one race is attributable to associated effects of one of the two other races. The three correlations involving race 72 were much smaller and only about 3–8% of the variability in race 72 would be attributed to associations with one of the other three races.

The large values of the pairwise correlations among races 40, 61, and 74 suggested a three-way association among factors controlling the disease reaction of these three races, thus triply resistant or triply susceptible accessions are expected in excess frequency. To test this, we classified all accessions with disease indices above the world mean index value for a given race as resistant and all accessions with disease indices below the world index as susceptible. On multiple classification, 101 of 350 accessions were susceptible to these three races, whereas 63 accessions were resistant to the three races. Thus, assuming that these 350 accessions are a random sample from the entire barley species, we infer that three-way associations among resistance alleles occur in 164/350, or about half of the barley accessions, and that about 29% (101/350) of the barley accessions are susceptible to races 40, 61, and 74 (triply susceptible) and about 18% (63/350) are resistant to all three races (triply resistant). A total of 106 accessions were resistant or susceptible to all four races; among these 106 accessions, 40 were quadruply resistant and the remaining 66 were quadruply susceptible.

Similar associations between races were observed in earlier studies. Jackson et al (5) and Muona et al (9) found positive correlations in CCV and CCII between resistance to races 40, 61, and 74, with race 72 independent of the other races. Large fluctuations were found in correlation coefficients from generation to generation in both studies.

TABLE 3. Genetic diversity indices averaged over resistance of barleys from different geographical areas to four races of *Rhynchosporium secalis*

Location	Within accessions	Within countries	Within regions
N.W. Europe			
Finland	0.939	1.469	
Czechoslovakia	0.843	0.843	
Switzerland	0.788	0.788	
Sweden	0.891	1.545	
Denmark	0.867	1.453	
England	0.938	1.459	
Scotland	0.699	0.699	
Ireland	0.985	1.322	
Poland	0.846	1.401	
France	0.666	1.269	
Austria	1.321	1.321	
Region	0.866	1.390	1.537
S. Europe			
Spain	0.836	1.363	
Italy	0.642	1.193	
Romania	0.828	1.235	
Greece	0.813	1.132	
Region	0.744	1.232	1.408
USSR	0.852	1.363	1.363
S.W. Asia			
Cyprus	0.647	1.162	
Turkey	0.738	1.481	
Iraq	0.766	1.310	
Israel	0.800	1.406	
Region	0.745	1.381	1.472
M.S. Asia			
Iran	0.851	1.487	
Afghanistan	0.709	1.156	
India	0.709	1.269	
Nepal	0.728	1.071	
Region	0.754	1.296	1.359
E. Asia			
China	0.673	1.209	
Korea	0.709	1.091	
Japan	0.804	1.440	
Region	0.720	1.241	1.287
N. Africa			
Egypt	0.821	1.384	
Ethiopia	0.685	1.428	
Algeria	0.783	1.340	
Morocco	0.581	0.581	
Region	0.764	1.371	1.460
S. Africa	0.743	1.255	1.255
Australia	0.762	1.326	1.326
C. America			
Mexico	0.774	1.326	
Guatemala	0.834	1.172	
Region	0.800	1.260	1.309
S. America			
Peru	0.638	0.638	
Venezuela	0.667	0.907	
Chile	0.686	1.253	
Argentina	0.748	1.340	
Region	0.707	1.152	1.356
United States	0.785	1.477	1.477
World	0.777	1.325	1.407
			World total 1.462

TABLE 4. Allocation of genetic diversity for resistance to four races of *Rhynchosporium secalis* (Table 3) into components associated with various levels of the hierarchical geographical structure

Location	H_T	D_C	D_A	H_W
N.W. Europe	1.537	0.148 (9.61)	0.524 (34.08)	0.866 (56.31)
S. Europe	1.408	0.176 (12.48)	0.488 (34.64)	0.744 (52.88)
USSR	1.363	0	0.510 (37.44)	0.852 (62.56)
S.W. Asia	1.472	0.091 (6.17)	0.636 (43.24)	0.745 (50.59)
M.S. Asia	1.359	0.063 (4.62)	0.542 (39.87)	0.754 (55.51)
E. Asia	1.287	0.046 (3.58)	0.521 (40.45)	0.720 (55.96)
N. Africa	1.460	0.089 (6.13)	0.606 (41.54)	0.764 (52.33)
S. Africa	1.255	0	0.511 (40.77)	0.743 (59.23)
Australia	1.326	0	0.564 (42.51)	0.762 (57.49)
C. America	1.309	0.049 (3.72)	0.461 (35.20)	0.800 (61.09)
S. America	1.356	0.204 (15.03)	0.446 (32.86)	0.707 (52.11)
United States	1.477	0	0.691 (46.81)	0.785 (53.19)
World 1.462 = 0.055(3.78) + 0.082(5.59) + 0.548(37.50) + 0.777(53.12)[a]				

[a]The quantities in the bottom line are worldwide diversity ($H_T = 1.462$), distance among regions ($D_R = 0.055$), distance among countries ($D_C = 0.082$), distance among accessions ($D_A = 0.548$), and diversity within accessions ($H_W = 0.777$), respectively. The numbers in parentheses are percentage values represented by each component.

TABLE 5. Pairwise correlations between resistance of barley accessions in the world sample to four races of *Rhynchosporium secalis*

	Race 40	Race 61	Race 72	Race 74
Race 40	1.000			
Race 61	0.494	1.000		
Race 72	0.288	0.199	1.000	
Race 74	0.436	0.465	0.170	1.000
$r_{0.05} = 0.104$[a], $r_{0.05} = 0.135$[a]				

[a]Critical values for correlation coefficients at 0.05 and 0.01 probability levels, respectively.

Shifts in racial composition of the pathogen population were suggested by these authors as a hypothesis to explain the observed changes in associations between resistance to different races. A direct implication of this hypothesis to our results would be that the observed associations of resistance to different races were due to concurrence of these races for all the regions as a whole. This hypothesis also implies that plants grown in different geographical areas would show different patterns of association respecting the resistance to the four races, because it was unlikely that the pathogen populations have the same composition in different geographical areas. Our data showed that barleys from different areas had indeed established different patterns of resistance association. For example, among the 12 entries from Ethiopia (Table 2), three accessions were triply resistant, no entry was triply susceptible, and two accessions were quadruply resistant. It appears that the low disease index level of Ethiopian barley was mainly due to high resistance to individual races. The pattern was quite different for the Polish barley accessions (Table 2). Most of the accessions from that country displayed a relatively low level of infection by these four races: eight of the 12 accessions were quadruply resistant and one accession was susceptible to races 40, 61, and 74. It is also known that the ecological as well as climatic conditions are very different between these two countries. Thus, if the causal agent for the observed associations was the concurrence of the races, this would suggest that the pathogen population in Ethiopia was also highly differentiated, whereas the pathogen population in Poland was relatively uniform. However, data published thus far on studies of genetic variability in populations of *R. secalis* are insufficient for the inference of correspondence between resistance in the barley host and racial composition of the scald pathogen population in vast geographical regions.

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