Components of Slow-Rusting in Barley Infected with Puccinia hordei

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ABSTRACT

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In fast-rusting barley (*Hordeum vulgare*) cultivars Manker, Speciale, Larker, and Beacon, *Puccinia hordei* had a shorter latent period (days for 50% of the uredia to form), and produced more urediospores per square centimeter of leaf surface, more spores per uredium, more uredia per square centimeter of leaf surface, and larger uredia, than in the slow-rusting barleys MN 7572, MN 7544, MN 9062, and Rogers. The components of rust development were related to each other and to the area under the disease progress curve, as indicated by significant correlation coefficients.

Slow-rusting, a type of resistance known for many years (5, 21), has been described in *Avena byzantina* C. Kock, and *A. sativa* L. infected with *Puccinia coronata* Cda. f. sp. *avenae* Fraser & Led. (9, 19), *A. sterilis* L. infected with *P. graminis* Pers. f. sp. *avenae* Eriks. & E. Henn. (22), *Triticum aestivum* L. infected with *P. graminis* Pers. f. sp. *tritici* Eriks. & E. Henn. and *P. recondita* Rob. ex. Desm. f. sp. *tritici* Eriks. & E. Henn. (2, 23, 24), and *Hordeum vulgare* L. infected with *P. hordei* Otth. (4, 11).

Various components are involved in the slow development of disease. In barley infected with *Puccinia hordei*, some of the components are a lower infection frequency, a longer latent period, a lower sporulation rate, and a shorter sporulation period (4, 11, 12, 13). Similar components of slow development of disease have been demonstrated in other host-parasite relationships (6, 7, 8, 15, 17, 18, 20, 22).

This study, with some North American cultivars and lines of barley, was done to quantify latent period, infection frequency, size of uredia, and sporulation in fast- and slow-rusting barleys infected with *P. hordei*, and to investigate the relationship of these components to each other and to the area under the disease progress curve.

MATERIALS AND METHODS

The cultivar Rogers and the Minnesota lines MN 9062, MN 7572,and MN 7544, barleys that rusted slowly when infected with *P. hordei* in the field, and the cultivars Beacon, Larker, Manker, and Speciale barleys that rusted rapidly, were used to investigate components of slow-rusting in barley (*Hordeum vulgare* L.) infected with *Puccinia hordei* Otth. The barley cultivars were planted in the greenhouse on different dates so they would all be heading at the same time. The plants were inoculated as uniformly as possible in the boot stage of growth in a settling tower designed for inoculating adult cereal plants. The base of the tower was a rotating platform on which there were eight revolving disks on which the potted plants were placed. In the air above the rotating plants, a cloud of urediospores of *P. hordei*—race 23, was created with 5 mg of spores, with the aid of a carbon dioxide blast. The plants revolved in the cloud of urediospores for 5 min and then they were placed in a moist chamber for 16 hr and finally, in a greenhouse at about 21 ± 4 C. The experiment was designed as a randomized complete block in reference to placing the plants in the settling tower.

Plants were fertilized with a 10-10-10 (N-P-K) fertilizer 3 wk after planting and at the time of inoculation. Natural light supplemented with fluorescent lamps was used to provide a photoperiod of 16 hr per day. Experiments were done between September and December, 1976, when temperature, light, and relative humidity were relatively easy to control.

The latent period and the number of uredia per square centimeter of the upper surface on the flag and the second leaves were observed. The latent period was the time when 50% of the uredia had formed; uredia were counted each day after inoculation until no more developed. The number of uredia per square centimeter of leaf surface was determined from the total number of uredia on the upper surface of the two leaves divided by the area of the leaves. Area of leaves was calculated from length and width measurements using the formula for the area of a triangle (1/2 base × altitude).

Spores were caught in V-shaped metal trays placed immediately below the second leaf. The trays were 30 cm long, 18 cm wide (both slopes) and the angle of the V was 90 degrees. The trays were coated with Dri-slip (a product of 3M Company, St. Paul, MN 55101) and then buffed to reduce friction.

Urediospores were harvested at 2- to 3-day intervals from the time when sporulation began until the leaves were dead by gently tapping the infected leaves over the collection trays and then the trays were vibrated and

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brushed to transfer the spores into vials. Spores were weighed and then counted with a Coulter counter.

The weight of urediospores per uredium was calculated from the total weight of urediospores from the second leaf divided by the number of uredia on that leaf.

The size of uredia was determined by measuring the diameters, both parallel and perpendicular to the leaf veins, of nine uredia per leaf: three on the basal third, three on the middle third, and three on the tip third of the second leaf. The measured uredia were representatives of typical uredia on the leaf.

Analysis of variance and single-degree-of-freedom contrasts were computed to test differences between the fast- and slow-rusting plants. Differences among means were tested with Duncan's multiple range test.

The relationship of the components of slow-rusting, as measured in the greenhouse, to the area under the disease progress curve, as measured in the field, was studied.

To obtain data on the area under the disease progress curve, the cultivars Beacon, Larker, Manker, Speciale, Rogers, MN 9062, MN 7572, and MN 7544 were grown in hills (15 seeds sown per hill) in a randomized complete block design with ten replications at Rosemount, Minnesota in 1976. Border hills of Manker were inoculated with an oil suspension of urediospores of races 9 and 23 of *P. hordei* when the test plants were in growth stage 7 of the Romig scale [second node of stem formed, next-to-last leaf just visible (3)].

Rust severity was estimated with the aid of the modified Cobb's scale (14) four times during the course of the epidemic at weekly intervals. Evaluations began 5 days after the first uredia were seen in the plants (plants were heading at this time) and ended when the plants were ripe. The area under the disease progress curve (AUDPC) was computed using the Fortran IV subroutine AREA and the associated subroutine INTEG (1).

Regressions were computed with AUDPC as the dependent variable, and each of the components, measured in the greenhouse, as independent variables.

The relationship of latent period and uredia per square centimeter of leaf to AUDPC was further studied with 34 cultivars and lines. The latent period and uredia per square centimeter of leaf surface were measured on four to seven plants per cultivar or line in the greenhouse as previously mentioned between January and March 1977. Then the barleys were grown in hills (15 seeds/hill) in a randomized complete block design with three replications at both St. Paul and Rosemount, MN in 1977. Border hills of Manker were sown and inoculated and rust severity was estimated as mentioned above. Rust severity was noted three times in 1977 during the epidemic at Rosemount, beginning when most of the plants were in the boot stage of growth, and twice at St. Paul, beginning when the plants were in the soft-dough stage of growth. The AUDPC and regressions of AUDPC on latent period and uredia per square centimeter of leaf surface were then computed.

RESULTS

Components of slow-rusting.—Cultivars Rogers, MN 9062, MN 7572, and MN 7544 (the slow-rusting barleys) had significantly longer latent periods, fewer uredia per leaf, fewer spores per leaf, fewer urediospores per uredium, and smaller uredia than did the fast-rusting cultivars Beacon, Larker, Manker, and Speciale (Table 1). However, some components of slow-rusting resistance of individual slow-rusting cultivars or lines did not differ significantly from those of cultivars that rusted rapidly (Table 1).

The weight of urediospores per leaf and the number of urediospores per leaf were related as indicated by the fact that the correlation coefficient was 0.98 and significant ($P = 0.01$). One mg of spores contained approximately 1.6×10^5 spores.

The various components of slow-rusting shown in Table 2 were all significantly ($P = 0.01$) correlated with each other.

TABLE 1. Latent period, weight of urediospores produced per square centimeter of the surface of the second leaf, weight of urediospores produced per uredium, and number of uredia per square centimeter of the surface of the flag and second leaves when barley cultivars and lines that rusted slowly and rapidly were infected with *Puccinia hordei*[a]

Cultivars	Latent[b] period (days)	Spores/ cm² leaf[c] (mg)	Spores/ uredium[c] (mg)	Uredia/ cm² leaf (no.)	Size of[d] uredium (mm)[d]
Fast-rusting:					
Manker	8 ab	0.31 ab	0.094 ab	4.52 a	.8/.6 a
Speciale	7 a	0.59 a	0.138 a	5.86 a	.9/.5 a
Larker	7 a	0.38 a	0.148 a	5.09 a	.8/.5 ab
Beacon	7 a	0.47 a	0.132 a	3.99 a	.8/.5 ab
Slow-rusting:					
MN 7572	12 c	0.11 c	0.050 b	2.59 ab	.6/.4 bc
Rogers	13 c	0.09 c	0.080 ab	1.67 b	.5/.4 c
MN 7544	9 bd	0.12 bc	0.042 b	2.90 ab	.7/.4 abc
MN 9062	10 d	0.05 c	0.045 b	1.42 b	.5/.4 c

[a]Values are means of five replicates. Within a column, values with same letter are not significantly different at $P = 0.05$ according to Duncan's multiple range test.

[b]Latent period was the number of days from inoculation to when 50% of the uredia had formed.

[c]Spore count: 1 mg of urediospores was equal to 1.6×10^5 urediospores.

[d]The numerator and denominator are respectively the diameter of uredia measured parallel and perpendicular with the veins of the leaves.

TABLE 2. Correlation coefficients for the relationship between area under the disease progress curve (AUDPC) and various components of slow-rusting when barley lines and cultivars were infected with *Puccinia hordei*

Components	AUDPC	Latent period	Uredia per cm^2 leaf	Uredia size	Spores per uredium (mg)	Spores per cm^2 leaf (mg)
AUDPC	1.00	−.78	.92	.96	.85	.88
Latent period		1.00	−.78	−.76	−.81	−.84
Uredia/cm^2 leaf			1.00	.90	.82	.92
Uredia size				1.00	.82	.88
Spores/uredium (mg)					1.00	.90

Relationship of components of slow-rusting to AUDPC.—*Rosemount, 1976.*—The epidemic began when the eight cultivars and lines were heading and continued for 4 wk until the barley ripened. The initial rust severities of the entries ranged from 0 to 10% and the terminal severities ranged from 30 to 100%. The AUDPC values for fast-rusting Manker, Speciale, Larker, and Beacon were 721, 680, 671, and 656, respectively, and for slow-rusting MN 7572, Rogers, MN 7544, and MN 9062, were 381, 255, 253, and 180, respectively. The difference between the slow- and fast-rusting groups was statistically significant ($P = 0.01$).

The correlation coefficients (Table 2) indicate that AUDPC was related to each of the slow-rusting components.

During 1977 the study on the relationship of components of slow-rusting to AUDPC was repeated with 34 lines and cultivars. The barleys were tested for slow-rusting in the field at Rosemount and at St. Paul, and they were tested for latent period and uredia per square centimeter of leaf surface in greenhouse during the winter of 1977. In this study only the latent period and the number of uredia per square centimeter of leaf surface were related to AUDPC.

Rosemount, 1977.—The epidemic began when the barley was in the boot stage of growth and continued for 4 wk, until the barley was ripe. The initial rust severities ranged from 0 to 5% and the terminal severities ranged from 10 to 100%. The range of AUDPC for the entries varied from 52 to 480 with a mean of 241 (Table 3).

Latent period and uredia per square centimeter of leaf surface were both significantly ($P = 0.01$) related to AUDPC. The correlation coefficient was −0.80 for AUDPC and latent period, and 0.75 for AUDPC and uredia per square centimeter of leaf surface. Multiple regression of AUDPC, the dependent variable, and latent period and uredia per square centimeter of leaf surface, the independent variables, was significant ($P = 0.01$) and the coefficient of determination was 0.75.

St. Paul, 1977.—The epidemic began when the plants were in the soft-dough stage of growth and continued for 2 wk until the barley was ripe. The initial rust severities ranged from 0 to 20% and the terminal severities ranged from 5 to 100%. The AUDPC ranged from 17 to 320 with the mean being 203 (Table 3).

Latent period and uredia per square centimeter were again both significantly ($P = 0.01$) related to AUDPC. The correlation coefficient was −0.74 for AUDPC and latent period, and 0.58 for AUDPC and uredia per square centimeter of leaf surface. Multiple regression of AUDPC on latent period and uredia per square centimeter of leaf surface did not account for a significant amount of structure; the coefficient of determination was 0.56.

TABLE 3. The area under the disease progress curve (AUDPC) of barley lines and cultivars infected with *Puccinia hordei* at Rosemount and St. Paul, Minnesota, in 1977, and the latent period and uredia per square centimeter of the flag and second leaves when infected with *Puccinia hordei* in the greenhouse

Line	AUDPC[a]		Latent period[b]	Uredia/ cm^2 leaf[b]
	Rosemount	St. Paul		
MN4543	480	310	7.4	2.61
MN4588	460	330	8.2	1.23
MN4556	458	278	7.8	2.59
MN4581	412	390	7.9	1.27
MN4585	410	265	8.4	2.08
Cree	390	270	8.5	0.60
MN4564	388	225	8.9	1.30
MN4584	372	290	8.1	1.01
Larker	367	270	7.7	0.90
MN4573	347	235	8.5	2.10
MN4569	324	280	8.5	1.74
MN3307	322	160	8.3	1.25
MN5253	275	39	8.9	0.90
MN33290	220	270	10.1	1.42
MN4583	219	195	7.8	0.74
MN4582	218	320	10.3	0.50
MN33105	213	161	8.3	1.43
MN3340	212	128	11.7	0.66
MN5245	205	41	10.6	1.34
MN5293	183	33	12.5	0.54
Rogers	176	28	13.2	0.47
MN4559	173	135	10.3	0.71
MN3347	160	111	9.5	0.21
MN3318	149	101	11.2	1.60
MN5232	142	137	12.8	0.60
MN3371	138	136	13.8	0.14
MN3336	125	45	15.1	0.11
MN3353	115	121	9.8	0.08
MN5292	103	33	9.7	0.26
MN7544	103	63	12.9	0.28
MN5258	100	27	14.6	0.78
MN5259	91	17	13.3	0.28
MN5286	74	22	12.8	0.21
MN5206	52	39	14.1	0.29
LSD ($P = 0.05$)	65	83	1.2	.62

[a]Values are means of three replicates.
[b]Values are means of four-to-seven replicates.

DISCUSSION

The barley cultivars presently grown in Minnesota lack an adequate level of slow-rusting resistance against leaf rust because Beacon, Larker, and Manker, the most widely grown cultivars, rust rapidly. Our work identified sources of slow-rusting in some other cultivars and lines being developed at the University of Minnesota.

Several components, an extended latent period, small uredia, low numbers or uredia on leaves, and a low level of sporulation by the pathogen contributed to slow-rusting. Some of these components have been reported in slow-rusting cultivars of small grains infected with rust (4, 10, 11, 12, 22). However, not all cultivars that rusted slowly in our study differed from cultivars that rusted rapidly, as far as individual components of slow-rusting were concerned. This is not unusual, for example, some wheat cultivars contain two types or components of resistance to scab [caused by *Fusarium roseum* (Link) emend Snyd. & Hans. f. sp. *cerealis* (Cke.) Snyd. & Hans.], resistance to initial infection and resistance to the spread of the fungus within a plant, whereas other cultivars only contain one or the other of these components (16).

It is possible that the correlation coefficients that we report between components of slow-rusting in this study may be inflated because our lines were selected for slow-rusting before the study was made. The selection for slow-rusting would have concurrently tended to select the various components of slow-rusting. This was also suggested by Parlevliet and van Ommeren (13) and Ohm and Shaner (10).

Variation within each of the components studied was observed and it should be possible to select components of slow-rusting and develop lines of barley that possess them in desired combinations. Possibly latent period may be the easiest component to study and to use in a practical way. To determine latent period we counted uredia on the flag and second leaves, but latent period may be visually estimated and the test plants compared to known check lines.

Rapid progress could be made in breeding work by selecting slow-rusting lines in the field using the AUDPC, making the desired crosses with these lines, and then selecting long latent periods in the progeny in the greenhouse. This cycle could then be repeated until the desired lines had been developed.

It is not known why latent period and uredia per square centimeter of leaf area accounted for a significant amount of the structure of AUDPC at Rosemount but not at St. Paul in 1977. The data of Ohm and Shaner (10) suggest that the effectiveness of slow-rusting may be reduced after flowering. Since the lines and cultivars were infected much later (soft-dough stage) at St. Paul than at Rosemount (boot stage), differences in senescence may have influenced the degree of slow-rusting in some lines at St. Paul and not Rosemount.

In addition, the relatively poor epidemic that occurred at St. Paul in 1977 (as contrasted with the one at Rosemount) may have made it difficult to relate AUDPC to latent period and uredia per leaf area. The epidemic started late in the life of the plants at St. Paul and ended 2 wk later when the plants had matured. Thus, differences in AUDPC among the cultivars could not be readily detected because of the short period of time for the development of the epidemic.

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