Virulence of *Puccinia coronata* in Relation to Available Genes for Resistance in Oats

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ABSTRACT

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Isolates of *Puccinia coronata* collected in the United States during 1976–1980 were assayed for virulence on 32 oat (*Avena sativa*) cultivars and lines having different genes for resistance. Most of the isolates that had been collected on oats were virulent on cultivars Trispernia, Bondvic, and Ukraine. Average percentage of isolates virulent on the others ranged from 0.1 to 46%. Virulence among the isolates showed no tendency to increase on two components of Iowa multiline cultivars IA X421 and IA X434 but did increase significantly on another, IA X475. Of three southern cultivars of oats, virulence increased markedly on TAM 0-312, moderately on TAM 0-301, and did not increase on Coker 234. Virulence of isolates from buckthorn (*Rhamnus cathartica*) generally paralleled that of isolates from oats. The number of virulence combinations represented by the isolates from oats varied from 36 in 1978 to 86 in 1976. Coker 234 and FL 723A2 were shown to probably carry the same gene for resistance to the crown rust pathogen.

Crown rust of oats (*Avena sativa* L.) caused by *Puccinia coronata* Corda has been widespread in the United States and Canada (5) in recent years but has generally been light in severity. Significant losses, however, have occurred from time to time in certain areas. In 1978, a year relatively favorable for crown rust, losses in the major oat-producing states of Michigan, Minnesota, South Dakota, and Texas were estimated at 5, 2, 3, and 2%, respectively (David L. Long, *personal communication*). Much heavier losses occurred in small areas or in special situations (5), and crown rust remains a threat to efficient oat production.

The only economically feasible method for controlling crown rust is the use of resistant cultivars, and this method depends on the availability of sources of resistance. The objective of this study was to evaluate virulence of *P. coronata* in relation to available sources of resistance. The work was done from 1976 through 1980.

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MATERIALS AND METHODS

Three cultivars, Bondvic, Trispernia, and Ukraine, were included in the study because they were the only ones of the set of 10 differential cultivars used to identify races of *P. coronata* (12) that still had significant resistance to the fungus and also because they enabled us to relate the current *P. coronata* population to earlier populations. The remaining 29 cultivars and lines (henceforth referred to as lines) (Table 1) were all potentially useful sources of resistance to at least part of the *P. coronata* population. Ascencao was introduced from Brazil many years ago (10). Coker 234, FL 723A2, MN 5250, TAM 0-301, and TAM 0-312 all derived their resistance from lines of *Avena sterilis* L. collected in countries around the Mediterranean Sea or in the Near East.

Five lines designated "Pc" are part of an isogenic set developed in Canada (3). Four "IA" lines were developed in the Iowa multiline program (1), and the 14 "H" lines were also developed in Iowa. The "Pc," "IA," and "H" lines are all believed to carry single, distinct genes for resistance derived from strains of *A. sterilis* (14).

Cultures of *P. coronata* used in the study were collected from intensive oat-growing areas of the United States during the 5-yr period 1976–1980. A collection consisted of a few infected leaves of the same oat cultivar or buckthorn (*Rhamnus catharticus* L.) bush at one location. Collections were increased in bulk on the susceptible cultivar Markton to obtain vigorous urediniospores for inoculating

test plants. Single-uredinium cultures were isolated when needed to clarify host reactions obscured by different pathogenic biotypes in the same collection or to confirm or clarify significant or questionable observations.

General procedures and disease rating scales were the same as those described by Murphy (9).

RESULTS AND DISCUSSION

Virulence of isolates from oats. More than 90% of the isolates were virulent on Trispernia and Bondvic (which usually show similar reactions to *P. coronata*) and more than 80% on Ukraine over the 5-yr period (Table 1). About 90% of all isolates from 1976 through 1979 were virulent on Trispernia and Bondvic, but in 1980 this percentage increased to 97%. Virulence on Ukraine increased from 74% in 1976 to 89% in 1979 and 1980. The overall susceptibility of Trispernia and Bondvic to crown rust has been recognized for some time (8) and may be related to the fact that the Trispernia resistance has been used in some widely grown commercial oat cultivars. The resistance of Ukraine has not been used extensively in commercial cultivars; however, a gradual increase in virulence on it has occurred in the *P. coronata* population over the past 10–12 yr. The current level of virulence on these three cultivars makes them worthless for practical plant breeding.

Lines IA X421, IA X434, and IA X475 are components of Iowa multiline cultivars and have had approximately the same exposure to *P. coronata* populations in the field, but year to year patterns of virulence on them have differed. Percentages of virulent isolates were uniformly low on IA X421 and showed no consistent increase. Virulence on IA X434 did not change and was much higher than on IA X421. Virulent isolates on IA X475 steadily increased from 35 to 72% from 1976 to 1980.

Virulence on the Texas cultivars TAM 0-301 and TAM 0-312 changed. When released in 1974 (6,7), these two cultivars were regarded as resistant to all components of the crown rust population, but by 1976, some isolates of *P. coronata* could parasitize them. The number of isolates virulent on TAM 0-312 steadily increased until they constituted more than half of the population in 1980. The situation for TAM 0-301 was more complicated. The simple dichotomous division of pathogenicity into "virulent" and "avirulent" requires an artificial point of demarcation along a host reaction scale that includes all gradations between highly resistant (or immune) and highly susceptible. In the case of TAM 0-301, most isolates rated as virulent in Table 1 induced host reactions near the center of the pathogenicity scale, and the inexact classification was often arbitrary. In addition, virulence of such isolates was affected by temperature fluctuations in the greenhouse. We concluded that TAM 0-301 was not as susceptible to crown rust, relative to other lines, as the data in Table 1 indicate. We believe, however, that there is definitely a trend toward a greater percentage of isolates with virulence on TAM 0-301 in the *P. coronata* population.

Ascencao was introduced into the United States many years ago but has not been used extensively in the development of new cultivars. About 7% of all isolates were virulent on Ascencao over the 5-yr period. This is about twice the percentage noted for preceding years (8). The long-term trend indicates a gradual increase in virulence, which may relate to the observation that virulent isolates, although clearly on the virulent end of the pathogenicity scale, are seldom "fully virulent" on Ascencao.

Another group of lines characterized as resistant to all but a few crown rust isolates included Coker 234, FL 723A2, H 441, H 547, H 548, H 555, H 677, IA Y345, and MN 5250. Of these, Coker 234, FL 723A2, and H 555 showed less than full susceptibility to isolates rated as virulent on them. The rare isolates that attacked the others were fully virulent on them.

Virulence of isolates from buckthorn.

Table 1. Virulence of *Puccinia coronata* isolates from oats on lines and cultivars of oats having potentially useful genes for resistance

Cultivar or line	Gene[a]	Percent isolates virulent					Total no. of isolates	Overall percent isolates virulent
		1976	1977	1978	1979	1980		
Ascencao	Pc-14	3.3	4.3	12.4	6.7	5.6	1,651	6.6
Bondvic	···	92.3	91.3	89.8	92.0	97.4	1,630	92.9
Coker 234	Pc-61	0.3	0.9	1.0	0.0	0.0	1,604	0.4
FL 723A2	···	···	···	1.0	···	···	293	1.0
H 382	Pc-36	8.9	4.2	17.2	14.9	12.5	1,715	12.2
H 441	Pc-53	1.0	1.7	3.4	1.4	1.4	1,608	1.7
H 544	···	···	···	15.8	9.2	0.9	1,128	8.5
H 547	···	1.7	0.0	0.0	0.0	0.3	1,607	0.4
H 548	···	···	···	1.0	0.7	0.6	1,074	0.8
H 550	···	···	···	22.4	···	···	343	22.4
H 555	Pc-57	0.0	0.0	0.3	0.5	0.0	1,606	0.2
H 558	···	14.0	31.0	···	···	···	528	21.8
H 559	···	32.6	34.4	···	···	···	551	33.4
H 560	···	32.9	40.6	···	···	···	543	36.2
H 561	···	2.3	25.7	5.4	3.0	1.1	1,616	6.1
H 562	···	24.8	21.7	···	···	···	542	23.4
H 676	Pc-14 + 36	···	···	···	5.2	2.0	796	3.7
H 677	Pc-52 + 36	···	···	···	2.6	0.3	783	0.9
IA X421	Pc-52	2.0	2.6	6.0	5.9	2.0	1,626	3.9
IA X434	Pc-51	24.6	19.7	23.9	26.2	15.9	1,753	22.4
IA X475	···	34.8	34.4	47.3	40.0	71.9	1,758	46.2
IA Y345	···	···	···	0.0	0.0	0.3	1,072	0.1
MN 5250	···	···	···	0.0	0.0	0.3	1,020	0.1
Pc 38	Pc-38	1.7	0.0	2.0	3.7	4.2	1,625	2.6
Pc 39	Pc-39	1.3	2.1	1.4	1.6	0.6	1,610	1.4
Pc 45	Pc-45	19.2	29.2	···	···	···	551	23.6
Pc 46	Pc-46	23.9	22.0	···	···	···	563	23.1
Pc 50	Pc-50	6.2	1.3	15.1	10.2	7.1	1,684	8.5
TAM 0-301	Pc-58	2.0	1.3	6.4	3.5	10.8	1,607	5.0
TAM 0-312	Pc-59	6.6	12.3	21.7	25.9	55.6	1,684	26.3
Trispernia	Pc-6d	92.3	86.7	87.9	89.7	97.2	1,631	91.0
Ukraine	Pc-9	74.0	77.3	83.7	89.3	88.8	1,694	83.6

[a]Indicates designation of gene for resistance to *P. coronata* (11).

Table 2. Virulence of *Puccinia coronata* isolates from buckthorn on lines and cultivars of oats with potentially useful genes for resistance

Cultivar or line	Gene[a]	Percent isolates virulent in year					Total no. of isolates	Overall percent isolates virulent
		1976	1977	1978	1979	1980		
Ascencao	Pc-14	4.8	2,6	11.1	15.8	2.6	287	9.4
Bondvic	...	69.0	92.5	78.7	85.7	94.9	287	83.6
Coker 234	Pc-61	2.4	0.0	0.0	0.0	0.0	280	0.3
FL 723A2	...	...	...	0.0	...	...	69	0.0
H 382	Pc-36	13.6	5.0	14.7	32.3	38.5	297	22.2
H 441	Pc-53	0.0	0.0	0.0	5.4	0.0	281	1.8
H 544	Pc-57	...	...	8.7	19.8	0.0	204	12.3
H 547	...	7.1	0.0	0.0	0.0	0.0	280	1.1
H 548	...	...	...	0.0	0.0	0.0	199	0.0
H 550	...	...	...	17.1	...	...	76	17.1
H 555	...	0.0	0.0	0.0	1.1	0.0	280	0.3
H 558	...	4.8	33.3	...	...	...	81	18.5
H 559	...	28.6	41.0	...	...	...	82	35.4
H 560	...	16.7	38.5	...	...	...	81	27.2
H 561	...	9.3	7.3	2.9	1.1	0.0	283	3.5
H 562	...	22.7	12.2	...	...	...	85	17.6
H 676	Pc-14 + 36	...	...	...	13.0	0.0	131	9.1
H 677	Pc-52 + 36	...	...	...	1.1	0.0	130	0.7
IA X421	Pc-52	9.1	5.4	4.3	1.1	0.0	281	3.6
IA X434	Pc-51	11.6	38.6	17.1	10.9	34.1	296	19.9
IA X475	...	23.8	55.0	54.4	58.5	66.7	294	53.1
IA Y345	...	...	...	0.0	0.0	0.0	199	0.0
MN 5250	...	...	...	0.0	0.0	0.0	199	0.0
Pc 38	Pc-38	7.1	5.3	2.9	4.3	0.0	282	3.9
Pc 39	Pc-39	2.3	2.6	0.0	0.0	0.0	281	0.7
Pc 45	Pc-45	18.6	17.9	...	...	...	82	18.3
Pc 46	Pc-46	20.9	57.1	...	...	...	85	38.8
Pc 50	Pc-50	4.8	5.1	19.7	11.8	5.0	290	11.0
TAM 0-301	Pc-58	0.0	0.0	0.0	0.0	0.0	280	0.0
TAM 0-312	Pc-59	0.0	10.0	16.7	13.8	2.6	257	10.5
Trispernia	Pc-6d	69.0	95.0	74.3	80.6	92.3	288	80.9
Ukraine	Pc-9	66.7	64.3	85.3	70.2	73.8	298	73.2

[a] Indicates designation of gene for resistance to *P. coronata* (11).

Isolates of *P. coronata* collected from buckthorn in the northern states in May and June were first transferred to oats and then held at 4 C until fall. They were then increased and used to inoculate the test lines. With a few exceptions, virulence of these isolates paralleled that of isolates collected from oats (Table 2). These results are in agreement with previous work (13).

The percentage of aecial isolates virulent on H 382 was about twice that of uredinial isolates obtained directly from oats. This difference was especially pronounced in 1979 and 1980. Another difference of possible significance was evident in pathogenicity tests on TAM 0-301 and TAM 0-312. On TAM 0-312, only 10% of the aecial isolates were virulent on TAM 0-312 compared with 26% of the oat isolates. None of the aecial isolates were virulent on TAM 0-301, whereas 5% of the uredinial isolates from oats were virulent. These differences probably reflect mutations to virulence in populations in the southern United States, where TAM 0-301 and TAM 0-312 are grown, whereas all aecial isolates came from northern states where the populations were not under selection pressure exerted by the genotypes of these cultivars.

Virulence combinations. The preceding discussion has considered genes for virulence individually, but these actually occur in combinations in any given fungal isolate. Such combinations, or races, are the genetic units that interact with the genotype of the host plant. The numbers of different combinations (races) observed in the different years are shown in Table 3.

Combinations of genes for virulence in the rust population are of critical importance in practical plant breeding. A cultivar with two genes for resistance will be protected from a fungus population in which corresponding genes for virulence are present only in different isolates (4,15). It will have no protection from an isolate that carries the two corresponding genes for virulence in combination. Examples can be found in Table 4, which shows 36 virulence combinations and the prevalence of each among isolates collected from oats in 1978, a representative year. Cultivars Ascencao and IA X421 were resistant to all of the common virulence combinations and most of the rare ones; however, three isolates representing two virulence combinations parasitized both cultivars. Combining the two genes for resistance of these cultivars in one line would give no protection from these isolates. In contrast, a combination of genes for resistance from Ascencao and H 382, although either one alone conditioned susceptibility to certain isolates, would provide resistance to all isolates.

Identification of duplicate genes. A problem in developing cultivars with resistance to *P. coronata* is determining whether genes for resistance from different sources differ from each other. Conventionally, one crosses plants carrying the genes in question and checks F_2 and F_3 segregating progenies for segregation of the genes for resistance, which is slow and laborious. The same information can often be deduced from such data as presented here. If two lines or cultivars consistently show the same reactions to all isolates over a period of time, it is highly probable that the lines carry the same gene for resistance.

Coker 234 and FL 723A2 were tested in 1978. Both cultivars showed high levels of resistance to most isolates, moderate susceptibility reaction to several additional isolates, and an unusual, strongly necrotic reaction to several others. In view of these completely parallel reactions, we concluded that their genes for resistance were probably identical.

Table 3. Number of virulence combinations (physiologic or pathogenic "races") among isolates of *Puccinia coronata* collected from oat and buckthorn

Host source	Virulence combinations				
	1976	1977	1978	1979	1980
Oat	86	75	36	58	49
Buckthorn	25	20	19	38	16

Table 4. Virulence combinations of isolates of *Puccinia coronata* from collections made from oats in 1978[a]

Combination no.	No. of isolates	Virulent on lines or cultivars[b]	Combination no.	No. of isolates	Virulent on lines or cultivars[b]
1	2	2,3,7,8,9,11,12,15	19	1	7,8,9,10,16
2	8	2,7,8,9,10,13,14,15,24	20	2	7,8,9,13,15
3	1	2,7,8,9,10,15	21	1	7,8,9,13
4	1	3,4,7,8,9,11,12,15,18	22	2	7,8,9,15,16
5	4	3,7,8,9,12,13,15	23	3	7,8,9,15,22
6	1	3,8,9,12,13	24	23	7,8,9,15
7	1	6,7,8,9,11,16	25	1	7,8,9,16
8	1	6,7,8,9,13,15,16	26	6	7,8,9,22
9	1	6,7,8,9,15,16,22	27	81	7,8,9
10	1	6,7,8,9,15,16	28	1	7,9,15
11	2	6,7,8,9,16,20	29	1	7,9,22
12	5	6,7,8,9,16	30	2	7,9
13	1	6,7,13,16	31	1	7,15,16
14	3	6,7,16	32	9	7
15	2	6,8,9,11,15,16	33	1	8,9,10,11,15
16	1	7,8,9,10,14,15,24	34	1	8,9,11
17	7	7,8,9,10,15,24	35	6	8,9,15
18	29	7,8,9,10,15	36	6	8.9

[a] All isolates shown for 1978 in Table 1 are not included because of problems with isolate mixtures and incomplete data for some oat lines.

[b] Numbers refer to oat lines and cultivars: 1 = IA Y345, 2 = H 544, 3 = H 561, 4 = H 548, 5 = H 547, 6 = H 550, 7 = Ukraine, 8 = Trispernia, 9 = Bondvic, 10 = TAM 0-312, 11 = Ascencao, 12 = IA X421, 13 = H 382, 14 = H 441, 15 = IA X475, 16 = IA X434, 17 = Pc 38, 18 = Pc 39, 19 = Coker 234, 20 = FL 723A2, 21 = MN 5250, 22 = Pc 50, 23 = H 555, and 24 = TAM 0-301.

Although the evidence is not as strong, a similar case could be made for IA Y345 and MN 5250.

Several oat lines used in this study were resistant to crown rust over the relatively long testing period. It is tempting to suggest that genes conditioning the resistance might provide protection for a long time, but it was such thinking that led to the severe crown rust epidemics of the 1950s. A much wiser course would be to use these genes for resistance in accord with the principles of diversity elucidated during the past two decades (2). Specifically, they could be used in multiline cultivars (1), in cultivar mixtures, or in a diversity of pure-line cultivars (16). This approach should prevent serious losses from the disease and also conserve the effectiveness of genes.

A specific application of this type of study to the management of multiline cultivars was furnished by the performance of lines IA X421, IA X434, and IA X475, which were components of multiline cultivars developed in Iowa (1). IA X421 was resistant to most isolates in 1976 and showed no significant change over the next 4 yr. About a quarter of all isolates attacked IA X434 over the 5-yr period, with no indication of virulence increasing with time. Both strains would be effective in a multiline. IA X475, however, started the period showing susceptibility to one-third of the isolates and by 1980 was susceptible to 72% of them. For this reason, it should be removed from the multiline.

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