

Genetics of Pathogenicity in *Puccinia coronata*: The Host Range Among Grasses

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ABSTRACT

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The host range of eight forms of *Puccinia coronata* Cda. among 106 grass species in Israel was determined at the seedling stage. A few species were not susceptible to any of these cultures. Most species were susceptible to more than one culture and many were to all eight cultures. Many common hosts were found, which is very important for genetical studies and for the development of hybrid rust in the field. Grasses vary in responses to the various forms of the rust pathogen; some individuals within a species being susceptible to one form and others to another form of *P. coronata*. The simultaneous inoculation technique was very useful for identifying real common hosts. Host range for two forms was also determined at the adult stage. Many hosts reacted the same way at both stages. Some species, however, differed at the two stages, indicating some difficulties for further

studies, but also suggesting the possible importance in nature of disengagement between the reactions at both stages. Several new host species and even genera were found. The host range of *P. coronata* in Israel was found to be much wider than in all previous studies combined. Host ranges of the forms differed no more widely than did host ranges of races within one form. The use of host range of forms as an aid in the taxonomy of their hosts was invalid for *P. coronata* because of its very wide host range which represents all the tribes of the Festucoideae. It is postulated that the chance of the host's exposure to the pathogens' attack is as important in the evolution of host range as host phylogenetic relationships. The long-term association of hosts and parasites brought about this adaptation.

Additional key words: crown rust, wild host species, host taxonomy based on pathogenicity, adult plant reactions.

The host range of a pathogen is the criterion by which *formae speciales* are determined. Some investigators believe that host ranges may point to close evolutionary relationships between the hosts and/or between the physiologic forms of the parasite (19,28,29,35). Host range also may be useful for characterizing offspring of crosses between forms (16,25) and for analyzing the

genetic background for pathogenicity (26).

Previous studies of the host range of different forms of *P. coronata*, whether on an extensive or on a limited number of hosts from which they were isolated (4,10,13,21-24,33, and others), showed that no form was specific to the host species or even the host genus from which it was isolated ([31] and other references). Some crown rust pathogen forms had a narrow host range (f. sp. *agrostis*, *alopecuri*, *arrhenatheri*, *holci*, and *phalaridis*) while others had a wide host range (f. sp. *avenae*, *festucae*, and *lolii*) with some overlap

between them. A *P. coronata* culture was usually well adapted to the host from which it was isolated, and in many cases it was less well adapted (but still virulent) to other hosts (4,23,24). Some hosts were susceptible to only one form while others were colonized by several. Only one species, *Lamarckia aurea*, was reported to be a common host to several forms (6,13,33). The many investigations on host range of the *P. coronata* forms revealed that the host range is not limited to genera related to the host from which the culture was isolated. Some forms were virulent on hosts of four additional tribes (7,13,22,23,33) while more selective forms were virulent on hosts of one additional tribe.

Puccinia coronata f. sp. *avenae* was the main form previously investigated. About 280 physiologic races have been identified (M. D. Simons, *personal communication*). In some cases the host ranges of races of *P. coronata avenae* were determined also among wild grasses (Dinoor, *unpublished*; 4,24). Differences between host ranges of races among wild grasses were pointed out.

The objective of the present study was to determine the host ranges of the different forms of *P. coronata* among most of the grasses in Israel. Until now, only the host range of form *avenae* had been investigated in Israel (7). Several authors (1,7,9,11) have advocated studies of the dynamics of host/parasite relationships in natural ecosystems (5,30). A genetical study which will follow this article will contribute to the understanding of the dynamics of the genetical control of pathogenicity.

MATERIALS AND METHODS

Plant material. Host range was tested on 106 species of grasses belonging to 43 genera. These include most of the wild Gramineae in Israel, the cultivated cultivar Fulghum and two foreign species *Aegilops squarrosa* and *Lolium multiflorum*. In 101 species, seed of a single collection was used, in five others two collections were used. A group of 3–10 seedlings was used from each collection.

Cultures. Seven cultures of the forms of *P. coronata* from wild species (one for each form) and nine cultures of races of form *avenae* were used.

Descriptions of propagation and maintenance of hosts and parasites, inoculation techniques, scale of evaluation and other details have been described (8).

RESULTS

The host ranges of the different forms. The detailed information on the reactions of the 106 host species to the 16 *P. coronata* cultures is presented in Table 1. We consider a plant species to be a host even if only one individual of a sample was susceptible. The numbers of genera and species compatible with each rust culture are given at the bottom of Table 1. Some cultures have a very wide host range, for example form *festucae* attacks 75 species belonging to 41 genera. At the other extreme, form *arrhenatheri* attacked only 13 species in 12 genera. Apart from form *arrhenatheri*, the host ranges of all forms are very wide but still clearly differ from each other. In considering the results, the following four topics are of special interest:

Common hosts. Common hosts are important for genetical studies of pathogenicity by facilitating the propagation of hybrid rust pathogens. We found 11 species (belonging to 10 genera of 2 tribes) to be hosts of all eight forms (the species numbered 15, 16, 18, 42, 47, 49, 65, 94, 102, 104, and 111 in Table 1). The extent of overlapping host ranges between forms is shown in Table 2 which lists the number of hosts common to pairs of forms.

Since the response of individuals from a single sample of seed is sometimes variable we tested the host range with greater accuracy by inoculating individuals of a species simultaneously with seven forms (see Table 2 in Reference 8). Some species segregated independently in their response to different forms. Certain hosts, like *Avena longiglumis*, had some individuals which were susceptible to all seven forms, and the susceptibility to some of the forms was of the highest type. One host, *Vulpia membranacea*, was found to be uniformly highly susceptible to all seven forms and therefore was chosen to serve as a common host for the

propagation of hybrid rust pathogens in further work.

Resistant species. Only a few species were resistant to all of the 16 cultures that we used. Six belong to the subfamilies Arundinoideae, Eragrostideae, and Panicoideae in which it is very rare to find a host for *P. coronata* (31). In Israel five of these species grow in summer when *P. coronata* is very rare or nonexistent (7). Five other resistant species belong to the subfamily Festucoideae which includes most of the hosts of *P. coronata*. These five species belong to genera which include other species that are susceptible. All host genera from this subfamily include species susceptible to at least one of the forms of *P. coronata*.

Comparison of the host ranges found in our studies with those described elsewhere. A summary of the number of host genera in which susceptibility to the *P. coronata* forms was found here and elsewhere is presented in Table 3. Only those host genera tested both here and elsewhere are presented. Our cultures are single spore cultures and only one culture represents each form. The results summarized from the literature usually refer to more than one culture from each form and usually were not single spore cultures. Even so, in six of the eight forms compared, the host range in Israel was found to be much wider than in all other places combined. On the other hand, some forms from other areas are virulent on plants from genera in which we found no susceptible plants. For example, form *avenae* was virulent on *Holcus*, *Lagurus*, and *Triticum*, and form *arrhenatheri* was virulent on *Alopecurus*, *Phalaris*, and *Phleum*.

New host genera. The following genera are new hosts for *P. coronata* (the number of virulent forms is shown in brackets): *Ammochloa* (8), *Boissiera* (3), *Cutandia* (8), *Eremopyrum* (7), *Gastridium* (7), *Pilgerochloa* (7), *Schismus* (1), *Scleropoa* (2), and *Sphenopus* (6). We also found new host species within already known host genera.

Do evolutionary relationships between hosts reflect the evolutionary relationships between forms? Data from Table 1 are arranged in Table 4 to show how many host genera from each tribe of the subfamily Festucoideae were susceptible to each form. There is no restriction of any form to host genera of the tribe to which the original host genus belongs. Each form has hosts in all or most of the other tribes. One of the extremes with a narrow host range is the form *arrhenatheri*, which has even more hosts in the tribe Festuceae than in the tribe Aveneae to which *Arrhenatherum* belongs. Also, hosts common to all forms were found in all tribes within the subfamily Festucoideae. One may also examine similarities of host range between forms and try to relate the forms accordingly.

The host range of the forms *festucae* and *lolii* is similar, and their original hosts belong to one tribe, Festuceae. Form *holci* and form *avenae* were isolated from hosts of another tribe, Aveneae. Form *holci* is more similar in its host range to forms *festucae* and *lolii* than to form *avenae*. Thus, it seems impossible to deduce phylogenetic relationships among the *P. coronata* forms from their host ranges.

The host range of one form represented by several isolates. The host range of the eight isolates of form *avenae* was found to be different for each isolate (Table 1). We find hosts which are common to all eight isolates and other hosts which were susceptible to only some or one isolate. Within one host genus there were species susceptible to some isolates and other species were susceptible to other isolates. The number of host genera for each isolate is 23–30 and of host species is 36–48. The host range of the eight isolates combined is 35 genera and 65 species, which is much wider than for any of the single isolates. The host range of a form represented by one isolate is therefore only a partial range for that form.

In comparing the host ranges of isolates of different forms and host ranges of isolates of the same form we find no difference. There is no greater similarity between isolates of the same form than between isolates of different forms.

The form *avenae* isolates differed from each other in the number of oat cultivars susceptible to them much more than in the number of susceptible grass genera and species. There is no relation, however, between the range of virulence on oat cultivars and the range of virulence on wild grasses. Extreme differences in the

TABLE 1. Detailed information on the reactions^a of grasses at seedling stage to forms of *Puccinia coronata* in Israel

No.	Grass species	Tribe	Culture of <i>P. coronata</i> ^b														
			ag	al	ar	av									p	f	l
						202	203	263	264	276	277	286	A-4-1	A-8-1			
1	<i>Aegilops bicornis</i>	Hordeae	4	3C		2C*				2C-	4	2C	2C*	3A	3C+ 4	4	
2	<i>biuncialis</i>													2C-	2C- 3C		
3	<i>crassa</i>		3A	2C													
4	<i>kotschyi</i>		2A-	2C*									2C*	3A	2C* 3C	3A	
5	<i>longissima</i>		3C	2C*		1C*	2A		2A*	2C-	2C			3C	3C-	3C-	
6	<i>ovata</i>																
7	<i>peregrina</i>																
8	<i>sharonensis</i>																
9	<i>speltoides</i>		3C*	1C		2C*										1C*	
10	<i>squarrosa</i>												2C*				
11	<i>Agrostis verticillata</i>	Agrostideae	4										1C*	3C	3A+ 2C		
12	<i>Alopecurus myosuroides</i>	Agrostideae												3C	3C-	3C	
13	<i>utriculatus</i>		1C*	4					3C*	3B				2C*	3B-	3B	
14	<i>ventricosus</i>		3B	4		3B		3C*	3C	3B	3B			3A	3B+	3B-	
15	<i>Ammochloa palaestina</i>	Festuceae	2B*	4		4	3B*	3C	2B-		2		3B-	3B*	3B	3C 3C	
16	<i>Arrhenatherum palestinum</i>	Aveneae	4	4	3A*	4	4	3A	4	3B	4	4	3A	4	4	3B 4 4	
17	<i>Avena barbata</i>	Aveneae	3B-	2C*	4	3B	4	3A+	4	3B	4	4	3A+	3B	3C	2C* 3C 3C	
18	<i>longiglumis</i>			3C*	4	4	4	4	4	4	4	4	4	4			
19	<i>sativa</i>		4	4	3A	4	4	4	4	4	4	4	4	4	3C*	3C- 3C* 3C-	
20	<i>sterilis</i>					4	4	4	4	4	4	4	4	4			
21	<i>wiestii</i>					4	4	4	4	4	4	4	4	4			
22	<i>Boissiera squarrosa</i>	Festuceae											3C	3C-	2C*		
23	<i>Brachypodium distachyum</i>	Festuceae		2C-	2A			2C*									
24	<i>Briza maxima</i>	Festuceae	3B+										3C-		1C*	3C 3C- 3A* 3C*	
25	<i>minor</i>		3A+					3B								4 3C- 2C* 3C* 3C*	
26	<i>Bromus alopecurus</i>	Festuceae	3C	2C*		2C-		1A		3C		2C		2C*	3C+	3C* 4	
27	<i>brachystachys</i>		3C												2C-		
28	<i>danthoniae</i>		3C*	2C-		4	3B+	4	4	4	4	4	3C	3A	4	3A 4	
29	<i>fasciculatus</i>		4	2C		3B		2C*	2C	3C*				1C*	3B	3C* 3A* 4	
30	<i>japonicus</i>		3C	2B*										1C*			
31	<i>lanceolatus</i>		3C-														
32	<i>madritensis</i>		2C*														
33	<i>rigens</i>														3C	3A	
34	<i>rubens</i>															4	
35	<i>scoparius</i>		4	3C-											3C-	3C* 3A-	
36	<i>squarrosus</i>														3C-	4 2A	
37	<i>sterilis</i>		2C*														
38	<i>tectorum</i>														2C*		
39	<i>Cenchrus echinatus</i>	Paniceae													3C-	4 3C	
40	<i>Cornucopiae involucreatum</i>	Agrostideae	4	4		4	4		4	3B+	4	4	4	4	4	3C- 4 4	
41	<i>Cutandia maritima</i>	Festuceae	3B-			4	3C*	3C-	3B	4	1C-	4	3A	4			
42	<i>memphitica</i>		4	4	3A	4	4	4	3B*	3C*	4	4	4	4	4	4 4 4	
43	<i>philistea</i>		3B	4		3C	3C+	3C-	3C+	3C	3C	3C-	3B	2C*	4	3C 4 4	
44	<i>Cynosurus coloratus</i>	Festuceae	4	4		4	4	4	4	4	4	4	4	4	4	4 4 4	
45	<i>echinatus</i>		4	4		4	4	4	4	3B	4	4	4	3B	4	3B 4 3A	
46	<i>elegans</i>																
47	<i>Dactylis glomerata</i>	Festuceae	4	3C*	2C*	4	4	4	4	4	4	4	4	4	4	4 4 4	
48	<i>Dactyloctenium aegyptium</i>	Chlorideae															
49	<i>Echinaria capitata</i>	Festuceae	4	4	4	4	4	4	4	4	4	4	4	4	4	4 4 4	
50	<i>Eleusine indica</i>	Chlorideae															
51	<i>Elymus caput-medusae</i>	Hordeae	3C	2C-													
52	<i>geniculatus</i>		2C-	2C*		1C*								1C*	3A	3C 4 3A	
	<i>Eremopyrum</i>	Hordeae												1C*	3C	3C 4 3C	

(continued)

TABLE 1 (continued)

No.	Grass species	Tribe	Culture of <i>P. coronata</i> ^b																
			ag	al	ar	av								h	p	f	l		
						202	203	263	264	276	277	286	A-4-I					A-8-I	
53	<i>buonapartisi</i>		4	3A		4	2	4	3A	4	4	3A				4	3C*	4	4
	<i>Festuca</i>	Festuceae																	
54	<i>arundinacea</i>																	4	3B
	<i>Gastridium</i>	Agrostideae																	
55	<i>ventricosum</i>		4	4		4	4	4	4	3B+	4	4	4	3C	4	4	4	4	
	<i>Gaudinia</i>	Aveneae																	
56	<i>fragilis</i>		4	4		4	4	4	3B	4	4	4		3C	4	3C*	4	4	
	<i>Holcus</i>	Aveneae																	
57	<i>annuus</i>			1C*											4		4	4	
	<i>Hordeum</i>	Hordeae																	
58	<i>bulbosum</i>		2A	2C*											3C	2C*	3A	2C-	
59	<i>leporinum</i>			2A*		2C-								2C*		3A	2C-		
60	<i>marinum</i>		2C*												2C*	2C*			
61	<i>murinum</i>		3A-												2C*	3C-	3A	2C-	
62	<i>spontaneum</i>																	2C*	
	<i>Koeleria</i>	Aveneae																	
63	<i>phleoides</i>		4	4		4	2	4	4	4	2	3C		3B*	3A	3B	4	3A	
	<i>Lagurus</i>	Agrostideae																	
64	<i>ovatus</i>														3C*		2C*	3C-	
	<i>Lamarckia</i>	Festuceae																	
65	<i>aurea</i>		4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	
	<i>Lepturus</i>	Monermeae																	
66	<i>cylindricus</i>		3C-			3C*	3C			2C*	2C*		2C*					3A	
	<i>Lolium</i>	Festuceae																	
67	<i>gaudinii</i>		3B	3C			3B*							3B*	4		4	4	
68	<i>multiflorum</i>														4		4	4	
69	<i>perenne</i>			4											4		4	4	
70	<i>rigidum</i>		3B+	2C*						2C*		3B		4		3A	4		
71	<i>subulatum</i>		4	3C+	3A							3B-		3C*	4	3C*	4	4	
72	<i>temulentum</i>													1C*	4		4	4	
	<i>Oryzopsis</i>	Stipeae													4		4	4	
73	<i>caerulescens</i>		3B																
74	<i>miliacea</i>														2A		3A	3A*	
	<i>Phalaris</i>	Phalarideae																	
75	<i>brachystachys</i>																		
76	<i>bulbosa</i>		3C-												3A+	1C*	3C-	2A+	
77	<i>canariensis</i>					3C*				1C*	2B-				4	3A-			
78	<i>minor</i>		4	4		4	2C	2C*	3A*	3B	4	4		3A	3C	3A	2C*		
79	<i>paradoxa</i>		4	4		4	4	4	4	4	4	4	2C*	2C*	4	3A-	2		
80	<i>paradoxa</i>		4	4		4	4	4	4	4	4	4	3A+	3A+	3A-	4	4	4	
	<i>Phleum</i>	Agrostideae																	
81	<i>subulatum</i>		3B	4		4	4	4	4	4	4	4	4	4	3B	4	4	4	
	<i>Pholiturus</i>	Monermeae																	
82	<i>filiformis</i>								3A	4	2B	4	3A	3C					
83	<i>incurvus</i>		4	4		4	4	4	4	4	4	4	4	4	3A+	4	4	3A+	
84	<i>incurvus</i>		4	4	1C*	4	4	4	4	4	4	4	4	4	4	4	4	4	
	<i>Pilgerochloa</i>	Aveneae																	
85	<i>blanchei</i>		4	4		4	4	4	4	3B+	4	4		4	2C-	3C-	3C-	3A+	
	<i>Poa</i>	Festuceae																	
86	<i>exilis</i>		3B*	3B		4	3B	4	3A	3C+	4	4	3C	3C+	4	3B	4	3A	
87	<i>trivialis</i>		3A	2C*											3C-	3C*		3C-	
	<i>Polypogon</i>	Agrostideae																	
88	<i>maritimus</i>		4	3B		4				3C*					4	2C-		3C*	
89	<i>monspeliensis</i>		4	1C*			3B*								4		3B-	4	
	<i>Psilurus</i>	Hordeae																	
90	<i>incurvus</i>		4	4		4	4			3C*	4	4	3C	4	3B	3B	4	4	
91	<i>incurvus</i>		4	4		4	4	4	4	4	4	4	4	4	4	4	4	4	
	<i>Schismus</i>	Danthonieae																	
92	<i>arabicus</i>											2B-	2C*						
93	<i>barbatus</i>																		
	<i>Sclerochloa</i>	Festuceae																	
94	<i>dura</i>		4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	
	<i>Scleropoa</i>	Festuceae																	
95	<i>rigida</i>														4		4		
	<i>Secale</i>	Hordeae																	
96	<i>montanum</i>		2C-			2A*	1A*								2C*		3C*	3C-	1A
	<i>Setaria</i>	Paniceae																	
97	<i>verticillata</i>																		
	<i>Sorghum</i>	Andropogoneae																	
98	<i>halepense</i>																		
	<i>Sphenopus</i>	Festuceae																	
99	<i>divaricatus</i>		4	4		3B	3B	3C*	4	4	3C-	3B	3B-	3B-	3B		4	2C*	

(continued)

TABLE 1 (continued)

No.	Grass species	Tribe	Culture of <i>P. coronata</i> ^b																			
			ag	al	ar	av											p	f	l			
						202	203	263	264	276	277	286	A-4-1	A-8-1	h							
100	<i>Stipa tortilis</i>	Stipeae																3C				
101	<i>tortilis</i>		2A																		2C*	
102	<i>Trisetum glumaceum</i>	Aveneae	4	4	3C+	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	
103	<i>koelerioides</i>		4	4		4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3C* 4	
104	<i>lineare</i>		4	4	3C*	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3B 4	
105	<i>lineare</i>		4	3A*			4	3A+	3A	2C*	3C	4		4	3						4 3C	
106	<i>Triticum dicoccoides</i>	Hordeae																			4	
107	<i>Vulpia aetnensis</i>	Festuceae	4	4		4	4	4	4	4	4	4	4	3A+	4	4	4	4	4	4	4	
108	<i>brevis</i>		4	4		3C	3C-	3C+	3C	3A	3C	3C	2C*	2C-	2C*	4	3C	3B	4	4	3C 3B	
109	<i>bromoides</i>		4	4		4	4	4	4	4	3B	4	3B	4	3C	4	4	4	4	4	4	
110	<i>membranacea</i>		4	4		4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	
111	<i>myurus</i>		4	4	3C*	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	
<i>Total number of genera with type 2 reaction</i>			37	31	12	29	30	26	26	29	27	29	23	28	38	32	41	38				
<i>with type 3 reaction</i>			2	4	2	3	4	1	1	3	3	1	3	3	2	2	1	3				
<i>with type 4 reaction</i>			10	6	6	3	6	6	6	9	2	6	7	10	16	17	12	14				
<i>with type 4 reaction</i>			25	21	4	23	20	19	19	17	22	22	13	15	20	13	28	21				
<i>Total number of species with type 2 reaction</i>			69	56	13	46	47	42	43	48	44	47	36	47	76	54	75	68				
<i>with type 3 reaction</i>			9	15	2	4	6	3	3	4	6	2	4	9	12	6	1	12				
<i>with type 4 reaction</i>			25	10	7	8	11	11	12	18	7	10	13	15	34	29	29	24				
<i>with type 4 reaction</i>			35	31	4	34	30	28	28	26	31	35	19	23	30	19	45	32				

^aThe triple coding system for host's reactions was previously described (8). In short, it is comprised of up to three signs: 0-4 = host reaction; A-C = types of nonuniform reactions, -, +, * = frequency of susceptible expression. 0 = highly resistant, 1 = very low compatibility, 2 = low susceptibility, 3 = medium susceptibility, and 4 = high susceptibility. A = mixed reactions on same leaf, B = segregation of plants in a sample, C = A + B. + = susceptibility predominates; - = resistance predominates; * = very low frequency of susceptibility.

^bAbbreviations of names for the *P. coronata* forms: ag = f. sp. *agrostis*; al = f. sp. *alopecuri*; ar = f. sp. *arrhenatheri*; av = sp. *avenae*; h = f. sp. *holci*; p = f. sp. *phalaridis*; f = f. sp. *festucae*; and l = f. sp. *lolii*.

TABLE 2. The number of common hosts (genera = g, and species = s) for pairs of forms (upper row vs left column)

Form	Form													
	al ^a		ar		av ^b		h		p		f		l	
	g	s	g	s	g	s	g	s	g	s	g	s	g	s
ag	30	52	11	12	28	41	34	59	31	50	36	57	35	57
al			12	13	27	40	30	53	29	44	30	51	30	50
ar					11	11	11	12	10	11	11	12	11	12
av							27	40	27	35	28	40	27	38
h									30	50	36	67	36	65
p											32	50	31	46
f													37	63

^aFor abbreviations of names for the rust forms see Table 1.

^bForm *avenae* (av) is represented only by culture A-8-1.

TABLE 3. The number of host genera compatible with the different forms of *P. coronata* in Israel and abroad

	No. of genera compatible with the following forms							
	ag ^a	al	ar	av	h	p	f	l
No. of host genera tested	18	14	15	29	15	10	17	24
No. of compatible hosts abroad	5	4	7	21	5	1	11	16
No. of compatible hosts in Israel	16	11	7	19	14	7	17	23

^aFor abbreviations of names for the host forms see Table 1.

number of susceptible species and genera between one form and another were larger than the extreme differences between races of one form. But for most races and forms these differences in the number of hosts were minute or nonexistent.

Adult plant reactions. The reactions of adult plants to two forms of *P. coronata* were determined to learn whether the description of

host/parasite relationships at the seedling stage also applies to later stages of host development. The same individual plants were tested at both stages. The data of the reactions of 86 species to form *alopecuri* and 97 species to form *phalaridis* is presented in Table 5. The classification of hosts in Table 5 is based on two criteria. 1, Adult vs seedling reaction: Susceptible at seedling stage and either susceptible or resistant at adult stage, and resistant as seedling and either resistant or susceptible as adult. 2, Segregation or no segregation of the individuals in a sample in response to the rust culture.

The main findings and conclusions are as follows:

Susceptibility at the adult stage. Adult susceptibility was found to be quite common. In some species all individuals were susceptible at both seedling and adult stages. In other species, even though the level of susceptibility declined, they were still susceptible as adults. In some species some individuals maintained their susceptibility while others were resistant as adults (these species are classified into groups a and b in Table 5). In some species susceptibility was expressed only in the adult stage (group d).

The adult plant host range. As shown before for the seedling

TABLE 4. The number of host genera, listed according to tribes, that were compatible with the different forms of *P. coronata* at the seedling stage

The form	Rust race	Tribe of original host	No. of compatible genera in the following tribes							
			Stipeae	Aveneae				Monermeae	Festuceae	Hordeae
				Agrostideae	Aveneae	Phalarideae				
ag ^a		Agrostideae	2	6	6	1	2	14	6	
al		Agrostideae	0	5	6	1	1	13	5	
ar		Aveneae	0	0	3	0	0	9	0	
av	202	Aveneae	0	4	6	1	2	12	4	
	203	Aveneae	0	5	6	1	2	12	4	
	263	Aveneae	0	3	6	1	1	13	2	
	264	Aveneae	0	4	6	1	1	11	3	
	276	Aveneae	0	5	6	1	2	12	3	
	277	Aveneae	0	4	6	1	2	11	3	
	286	Aveneae	0	4	6	1	1	13	3	
	A-4-1	Aveneae	0	3	3	1	2	11	2	
	A-8-1	Aveneae	0	4	6	1	1	12	4	
h		Aveneae	2	7	7	1	1	15	5	
p		Phalarideae	0	5	6	1	1	13	6	
f		Festuceae	1	7	7	1	2	16	7	
l		Festuceae	2	7	7	1	1	15	5	
Total no. of genera tested			2	7	7	1	2	17	7	

^aFor abbreviations of names for the rust forms see Table 1.

TABLE 5. Reactions of seedlings and adult grasses to two forms of *P. coronata*

Group	Seedling	Adult	Reaction to			
			<i>f. sp. alopecuri</i>		<i>f. sp. phalaridis</i>	
			Behavior of sample		Behavior of sample	
			Uniform	Segregating	Uniform	Segregating
a	S	S				
	4	4	13 ^a ,14,49,67,94	12,65,85,109	76,80,86,91,108,109,110,111	24,40,43,49,78,90
	3	3	71,105	22,84	29	1,34,51,83
	4	3	18,40,78,108	42,83,102,103,111	42,77,79,84,94	40,45,47,49,65,77,78,90,107
	4	2		79,80,91	44	
	3	2				1,12
b	S	R				
	4	0;0	53,55,56	42,43,63,69,79,83,91,102,103,109	55	18,43,47,65,81,107
	4	1	81,107	43,63,111		
	3	0;0	86,88	12,35,84	52	1,3,45,51,61,83
	3	1	1	22,45		
	2	0;0	58	3,4,28		58
	2	1	51			
c	R	R				
	1	0;0	47		75	
	0	1		45		
	0;0	0;0	2,6,7,8,11,15,20,21,23,24,25,27,30,31,33,34,36,37,41,46,54,60,61,62,64,66,68,72,73,75,76,77,82,92,95,99,100,101	3,4,28,35,45,65,69,70,83,89	4,5,6,7,8,9,10,11,13,14,17,20,21,23,25,27,28,30,31,32,33,35,36,37,41,46,53,56,57,59,60,62,63,64,66,67,68,70,71,72,73,82,87,89,92,95,98,99,101,105,106	2,3,12,18,34,43,45,58,61,77,103
d	R	S				
	0;0	4		80,85	88,103	40,103
	0;0	3		22,70	16,85	2,24,26,45,81
	0;0	2		63	51	26

^aNumbers according to Table 1.

stage the host range at the adult stage for both forms covered genera of six different tribes. The two forms were similar in this respect.

Host ranges at adult vs seedling stages. Table 5 shows that in an appreciable number of host species individual plants reacted differently to *P. coronata* forms in the seedling and adult stages. However, when all the tested species were classified as either susceptible or resistant (based on the criterion that a species in

which we find a susceptible individual is classified as susceptible) most of them were classified similarly whether on the basis of seedling or adult reactions (80% for form *alopecuri* and 85% for form *phalaridis*). Host species having some individuals susceptible at both stages were classified as susceptible, regardless of whether other individuals within the sample had different reactions in the seedling and adult stages.

Variability between individual plants within a species. In some

species, seedlings were uniform in response while adult plants grown from the same seedlings segregated in their response. Based on its reaction to form *alopecuri*, *Vulpia bromoides* (no. 109 in Table 1), was classified in both groups a and b under segregating species. This means that all seedlings tested were susceptible while some of the adults were susceptible (group a) and some were resistant (group b). Similarly, *Lolium rigidum* (no. 70 in Table 1) was uniformly resistant at the seedling stage but segregated at the adult stage [groups c and d].

Specificity in seedling susceptibility turning into adult resistance. Seedling-susceptible *Avena longiglumis* (no. 18 in Table 1) turned resistant in the adult stage to form *phalaridis* but remained susceptible to form *alopecuri*. On the other hand, adult *Poa exilis* (no. 86 in Table 1) remained susceptible at the adult stage to form *phalaridis*, but became resistant to form *alopecuri*.

DISCUSSION

Certain aspects of our studies on host range have already been discussed (8). In this present study we extended our work to cover a wider range of grass species in Israel. The main reason was to assemble background information so that our genetical studies will reveal a broader range of effects of the genes for pathogenicity.

The existence of hosts common to more than one form is important not only for the propagation of hybrid rust pathogens in genetical work. It might be of much importance in nature for the propagation and spread of hybrid rust fungi that occasionally are produced on the common alternate host *Rhamnus palaestina*. Somatic recombination has been demonstrated in rust fungi (3,20,34), including *P. coronata avenae* (2); therefore, it is not unlikely that common main hosts also will serve as an appropriate background for asexual recombination between forms of *P. coronata*.

Variability in the reaction between individuals of the same host species was demonstrated here on a large range of hosts. The validity of a species serving a common host for two or more forms may, therefore, be questioned, since individuals susceptible to one form may not be the same ones susceptible to the other forms as well. The use of the simultaneous inoculation technique enabled us to detect individual plants that were susceptible to more than one form. We have shown that there are some individual plants of *Avena longiglumis* and of *Vulpia membranacea* that are common hosts for seven forms of *P. coronata*. Common hosts for several forms were also found among individual plants of other species (8 and unpublished).

Another important aspect of host range studies is the relation between host response at seedling vs adult stages. Most studies, including our own, relate to seedling stage because of technical convenience. It would be reasonable to assume that adult reaction would be the most important in determining the success or failure of that host in nature. We do not know the role of seedling reaction in stands of wild plants. The contribution of a healthy or less infected seedling to the establishment of a vigorous adult plant has not been studied in natural plant communities. We think that the existence of seedling resistance coupled with adult susceptibility points out the importance of separation between the two characters with emphasis on the selective advantage of dual behaviour of the host. We have no idea yet about the importance in nature of seedling being susceptible or resistant. The data presented here concerns the reactions of many hosts to only two forms at the seedling vs the adult state. Seedling reaction to form *avenae* in this study can be compared to adult reactions to the same form (7). These comparisons show that for many hosts, seedlings and adults react similarly. For this reason and for technical convenience we propose that for many of the species studied by us it is sufficient to describe seedling reactions, and to surmise reactions at the adult stage.

Host range studies also have been employed as an aid in the taxonomy of plants, and sometimes their parasites (19,28,29,35). Several authors have stressed the importance of taxonomy based on pathology (1,17,36). The rationale behind this approach is that the evolution of hosts and parasites is mutually reflected in each

other. Some host range analyses were based on data assembled from different sources and even included dried herbarium material (17,35). Our own analyses, and others carried out in Israel (9,11), are based on inoculations with each of the forms on a very large range of plants. We consider host ranges derived in this way to be more reliable.

Gerechter-Amitai (11) studied the host range of *Puccinia graminis* among cereals and grasses and concluded that the host range of stem rust forms is not a reliable taxonomic aid even though a few of his examples show a relation between host range and taxonomy. Anikster and Wahl (1) used these examples to support their conclusion that host range serves as a taxonomic aid. Gerechter-Amitai's results include examples both for and against this view: Some hosts within a tribe which were unique in their susceptibility were transferred to another tribe on taxonomical grounds (32) and thus ceased to be unique. Other host species that were unique in being the only susceptible one in their tribe cannot be moved, on taxonomic grounds, to another tribe. One may find differences between tribes in the proportion of genera susceptible to one rust pathogen form or another, but the presence of even a few susceptible genera within a tribe invalidates host reaction as an indication of taxonomic affiliation. This conclusion contradicts other opinions (34,35). Kenneth (17) has also advocated the use of host range in clarifying taxonomic controversies in hosts and parasites, but at the level of host subfamilies and pathogen genera rather than host tribes and pathogen forms. Within the Gramineae, the subfamilies may reflect not only phylogenetic distance, but differences such as day length requirement, stem vascularization, chloroplast structure, photosynthetic pathway, the chemical constitution of carbohydrate reserves and leaf anatomy (36) as of these that separate festuroids from nonfesturoids. We think that seasonal and ecological differences are an important component of these differences between festuroids and nonfesturoids. Only the Festucoideae grow in winter and spring while the rest grow mainly in late spring and summer. This seasonal-ecological difference may be very important in determining opportunities for parasites and thus be an additional barrier for the expansion of host range. Leppik (19) introduced the concept of biogenic radiation into the analysis of the phylogeny of rust fungi, including *P. coronata*. According to him the alternate host is in a pivotal position. The rust radiates from it onto many different main hosts, irrespective of whether they are related phylogenetically, seasonally, or geographically. Leppik (19) placed no phylogenetic, seasonal, or geographical restrictions on the biogenic radiation from the alternate to any particular main host.

The host range of *P. coronata* in Israel is very wide. A single spore culture covers here a much wider range of hosts than the range covered by all other isolates studied elsewhere in the world, combined. Our list of grass genera tested, according to tribes, relies mainly on the classification by Stebbins and Crampton (32). Genera not included in that classification were listed according to previous classifications (14,27). The data in Table 4 show that none of the forms is restricted to hosts within the tribe of the original host. The host range of any of the eight forms of *P. coronata* studied covers most if not all of the tribes. Therefore, there is no relation between the classification of grass genera into tribes and the host range of any form of *P. coronata*.

This great overlap of host range is not difficult to accept if we take account of the fact that the boundaries between tribes within the Festucoideae is indistinct (36). *P. coronata* seems to be specific to the festuroids, but there are exceptions. The genus *Schismus*, no longer placed in the Festucoideae, was unexpectedly susceptible to *P. coronata*. In this case it is probably the climatic factor which may have brought *Schismus* in contact with *P. coronata* of Festucoideae despite its phylogenetic distance from this subfamily. Similar results were obtained for the reaction of *Schismus* to stem rust (11) and powdery mildew (Eshed and Wahl, unpublished).

There is good reason to believe that *P. coronata* is an ancient parasite of grasses. Green (12) was of the opinion that a wide host range is a feature of an ancient parasite and that the evolutionary trend is towards more strict specialization. He coupled wide host range with low aggressiveness. However, our findings suggest that

this is not true for *P. coronata*. A wide host range can also be a more flexible situation. *P. coronata*, alternating between a recent main host and a less recent secondary host, is considered to be, as such, a more flexible species of rust (15,18). For these and other reasons the pathogenicity of *P. coronata* is extremely ramified among hosts. The evolutionary path for the development of its hosts is blurred. We maintain that the specificity of host/parasite relationships reflects the many random events that accompany host development in a region and in seasons where the parasite is very active. The history of a host's invasion into a pathogen's territory or alternatively, a pathogen's invasion into a host's territory, may affect the host range of a pathogen just as much as the phylogenetic relationships among hosts and among parasites with no geographical or seasonal proximity.

LITERATURE CITED

- Anikster, Y., and Wahl, I. 1979. Coevolution of the rust fungi on Gramineae and Liliaceae and their hosts. *Annu. Rev. Phytopathol.* 17:367-403.
- Bartos, P. G., Fleischmann, G., Samborski, D. J., and Shipton, W. A. 1969. Studies on asexual variation in the virulence of oat crown rust, *Puccinia coronata* f. sp. *avenae*, and wheat leaf rust, *Puccinia recondita*. *Can. J. Bot.* 47:1383-1387.
- Bridgman, G. H., and Wilcoxson, R. D. 1959. New races from mixtures of urediospores of varieties of *Puccinia graminis*. *Phytopathology* 49:428-429.
- Brown, M. R. 1937. Study of crown rust, *Puccinia coronata* Corda, in Great Britain. *Ann. Appl. Biol.* 24:504-527.
- Browning, J. A. 1974. Relevance of knowledge about natural ecosystems to development of pest management programs for agroecosystems. *Proc. Am. Phytopathol. Soc.* 1:191-199.
- Dietz, S. M., and Clokey, I. W. 1924. *Achyrodes aureum* (L.) Kuntze, a host for many rusts. (Abstr.) *Phytopathology* 14:36-37.
- Dinoor, A. 1967. The role of cultivated and wild plants in the life cycle of *Puccinia coronata* Cda. var. *avenae* F & L and in the disease cycle of oat crown rust in Israel. Ph.D. thesis, The Hebrew University, Jerusalem.
- Eshed, N., and Dinoor, A. 1981. Genetics of pathogenicity in crown rust: Physiological specialization into forms. *Phytopathology* 71:000-000.
- Eshed, N., and Wahl, I. 1970. Host ranges and interrelations of *Erysiphe graminis hordei*, *E. graminis tritici* and *E. graminis avenae*. *Phytopathology* 60:628-634.
- Gäumann, E. 1959. Die Rostpilze Mitteleuropas. Pages 569-579 in: Beiträge zur Kryptogamenflora der Schweiz. Buchdruckerei Buehler, Bern. 1407 pp.
- Gerechter-Amitai, Z. K. 1973. Stem rust, *Puccinia graminis* Pers., on cultivated and wild grasses in Israel. Ph.D. thesis, The Hebrew University, Jerusalem.
- Green, G. J. 1971. Hybridization between *Puccinia graminis tritici* and *Puccinia graminis secalis* and its evolutionary implications. *Can. J. Bot.* 49:2089-2095.
- Hassebrauk, K. 1962. Uredinales. Pages 240-248 in: Handbuch der Pflanzenkrankheiten. Dritter Band. Paul Parey, Berlin. 747 pp.
- Hitchcock, A. S. 1950. Manual of the grasses of the United States. 2nd ed. (revised by A. Chase). U.S. Dep. Agric. Misc. Publ. 200. 1051 pp.
- Jackson, H. S. 1931. Present evolutionary tendencies and the origin of life cycles in the Uredinales. *Mem. Bull. Torrey Bot. Club.* 18:5-108.
- Johnson, T. 1949. Intervarietal crosses in *Puccinia graminis*. *Can. J. Res. (C)* 27:45-65.
- Kenneth, R. 1979. Host range as a tool in determining taxonomic relationships within Gramineae and in some of their fungal foliar diseases. *Phytoparasitica* 7:1.
- Leppik, E. 1953. Some viewpoints on the phylogeny of rust fungi. I. Conifer rusts. *Mycologia* 51:512-528.
- Leppik, E. 1967. Some viewpoints on the phylogeny of rust fungi. VI. Biogenic radiation. *Mycologia* 59:568-579.
- Luig, N. H., and Watson, I. A. 1972. The role of wild and cultivated grasses in the hybridization of *formae speciales* of *Puccinia graminis*. *Aust. J. Biol. Sci.* 25:335-342.
- Massenot, M. 1965. Experimentation réalisée à Grignon sur la rouille couronnée des graminées (*Puccinia coronata* Cda.). *C. R. Hebd. Séances Acad. Agric. Fr.* 51:445-449.
- Melhus, I. E., Dietz, S. M., and Willey, F. 1922. Alternate hosts and biologic specialization of crown rust in America. *Iowa Agric. Exp. Stn. Res. Bull.* 72:207-236.
- Mühle, E. 1959. Zur Frage des Resistenzverhaltens der Gräser gegenüber bakteriellen und pilzlichen Krankheitsregnern. *Biol. Zentralbl.* 78:622-630.
- Murphy, H. C. 1935. Physiologic specialization in *Puccinia coronata avenae*. U.S. Dep. Agric. Tech. Bull. 433.
- Nelson, R. R. 1970. Genes for pathogenicity in *Cochliobolus carbonum*. *Phytopathology* 60:1335-1337.
- Nelson, R. R., and Kline, D. M. 1962. Intraspecific variation in pathogenicity in the genus *Helminthosporium* to gramineous species. *Phytopathology* 52:1045-1049.
- Post, G. E. 1932-33. Flora of Syria, Palestine and Sinai. Vol. II. Beirut, American Press. 928 pp.
- Savile, D. B. O. 1954. The fungi as aids in the taxonomy of the flowering plants. *Science* 120:583-585.
- Savile, D. B. O. 1971. Co-ordinated studies of parasitic fungi and flowering plants. *Le Naturaliste Can.* 98:535-552.
- Shattock, R. C. 1977. The dynamics of plant diseases. Pages 83-107 in: J. M. Cherrett and G. R. Sager, eds. *Origins of pest, parasite, disease and weed problems.* 18th Symp. Br. Ecol. Soc. Blackwell Sci. Publ. Oxford, London, Edinburgh and Melbourne. 413 pp.
- Simons, M. D. 1970. Crown rust of oats and grasses. *Am. Phytopathol. Soc. Monogr.* 5. 47 pp.
- Stebbins, G. L., and Crampton, B. 1961. A suggested revision of the grass genera of temperate North America. *Recent Adv. Bot. (from IX Int. Bot. Cong. Montreal, 1959) Univ. Toronto Press* 1:133-145.
- Straib, W. 1952. Beiträge zur Kenntnis der an Futtergräsern auftretenden Rostpilze. *Zentralbl. Bakt. Abt. 2, 107:1-39.*
- Watson, I. A., and Luig, N. H. 1959. Somatic hybridization between *Puccinia graminis* var. *tritici* and *Puccinia graminis* var. *secalis*. *Proc. Linn. Soc. N.S.W.* 84:207-208.
- Watson, L. 1972. Smuts on grasses: some general implications of the incidence of Ustilaginales on the genera of Gramineae. *Quart. Rev. Biol.* 47:46-62.
- Watson, L., and Gibbs, A. J. 1974. Taxonomic patterns in the host ranges of viruses among grasses, and suggestions on generic sampling for host range studies. *Ann. Appl. Biol.* 77:23-32.