Physiologic Specialization of *Puccinia hordei* in Israel from 1983 to 1985

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ABSTRACT

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In Israel, the rust pathogen *Puccinia hordei* annually attacks indigenous wild *Hordeum* species and cultivated barley. The sources of primary inoculum are indigenous alternate hosts, *Ornithogalum* spp. Studies on physiologic specialization of 299 rust cultures isolated from 1983 through 1985 revealed 67 virulence patterns. Some highly virulent cultures were of countrywide occurrence. Gene *Pa*7 offered protection against over 99% of the cultures, while genes *Pa*3 and *Pa*9 were effective against 47.16 and 42.8%, respectively. The overall virulence situation of cultures obtained during 1983–1985 deviated in some aspects from that of previous years. This could be seen in differences of the order of ranking of the virulence patterns as well as in the appearance of new virulence spectra. Assumably, the virulence situation of *P. hordei* is dynamic as a result of genetic recombination in the commonly occurring gametophytic stage of the fungus on widespread *Ornithogalum* spp.

Barley (*Hordeum vulgare* L.) is distributed worldwide and is important as animal feed and in human consumption. It is a particularly valuable crop in marginal lands because of its drought resistance (18), short growing season, and tolerance to soil salinity. Its role in integrated crop-livestock systems in North Africa and the Middle East goes far beyond grain production because the economic importance of straw may be equal or even exceed that of grain in some areas (17,22).

Leaf rust of barley caused by *Puccinia hordei* Otth can be a severe disease, as was particularly evident during 1974–1980 in many countries. It was damaging in Morocco (5) and Egypt, especially in the humid region of the Delta's northern area (9,20). Since 1970, the intensification of barley cultivation in cool and temperate regions has resulted in a considerable increase of barley leaf rust in the United Kingdom, Denmark, northwestern Europe, and New Zealand (8).

Breeding for resistance is the most recommended means to control barley rust (16). The population of *Hordeum spontaneum* K. Koch indigenous to Israel constitutes an abundant and very diverse gene pool for leaf rust resistance (3,13,15). Both low reaction and slow rusting resistance are available in this gene pool (13), and serve as important sources of resistance in breeding programs in various countries (14). Because virulence studies monitor virulences and virulence combinations in the pathogenic populations, they provide useful information for selecting effective resistance genes for epidemiological studies and modelling of epidemics (12).

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Studies conducted in Israel in the past years (2) have shown that some virulence patterns were particularly common each year, countrywide, and that a number of isolates rendered ineffective all known genes for specific resistance. Notably, the cultivars Gold (*Pa*4) and Egypt (*Pa*8) were susceptible to all isolates tested.

The objective of this study was to

Table 1. Virulence patterns in *Puccinia hordei* isolates collected in 1983, 1984, and 1985

Virulence patterns	Sudan *Pa*	Reka 1 *Pa*2+	Quinn *Pa*2+*Pa*5	Bolivia *Pa*2+*Pa*6	Egypt 4 *Pa*8	Peruvian *Pa*2	Gold *Pa*4	Estate *Pa*3	Cebada Capa *Pa*7	No. of isolates 1983	1984	1985	Total
1-1	S	S	S	S	S	S	S	S	R	33	18	19	70
1-2	S	S	S	S	S	S	S	R	R	14	18	6	38
1-3	S	S	S	S	S	R	S	R	R	3	1	1	5
1-4	S	S	S	S	S	S	R	S	R	1	1	3	5
1-5	S	S	S	S	S	S	S	S	S	1	0	0	1
1-6	S	S	S	S	S	R	S	S	R	2	1	1	4
1-7	S	S	S	S	S	S	R	R	R	0	2	0	2
2-1	S	R	S	S	S	S	S	S	R	5	3	5	13
2-2	S	R	S	S	S	S	S	R	R	1	5	10	16
2-3	S	R	S	S	S	R	S	R	R	1	0	1	2
2-4	S	R	S	S	S	S	R	R	R	0	0	1	1
3-1	R	S	S	S	S	S	S	S	R	5	6	9	20
3-2	R	S	S	S	S	S	S	R	R	5	5	2	12
3-3	R	S	S	S	S	S	R	S	R	1	0	0	1
3-4	R	S	S	S	S	S	R	R	R	3	1	0	4
3-5	R	S	S	S	S	R	R	R	R	1	0	0	1
3-6	R	S	S	S	S	R	S	S	R	1	0	0	1
4-1	R	R	S	R	S	R	S	S	R	1	0	0	1
4-2	R	R	S	R	S	S	S	R	R	0	2	1	3
4-3	R	R	S	R	S	R	R	S	R	0	1	0	1
4-4	R	R	S	R	S	R	S	R	R	0	1	0	1
4-5	R	R	S	R	S	R	R	R	R	0	0	1	1
5-1	R	R	S	S	S	S	S	S	R	2	0	1	3
5-2	R	R	S	S	S	R	S	S	R	1	0	0	1
5-3	R	R	S	S	S	S	S	R	R	0	2	2	4
5-4	R	R	S	S	S	S	R	R	R	0	0	1	1
6-1	S	R	R	R	S	S	S	R	R	1	1	0	2
6-2	S	R	R	R	S	R	R	S	R	0	1	0	1
6-3	S	R	R	R	S	R	R	R	R	0	3	0	3
6-4	S	R	R	R	S	S	R	S	R	0	1	0	1
6-5	S	R	R	R	S	R	S	R	R	0	0	1	1
7-1	S	S	R	R	R	S	S	R	R	1	0	0	1
8-1	S	S	R	S	S	S	S	S	R	3	1	1	5
8-2	S	S	R	S	S	S	S	R	R	5	5	0	10
8-3	S	S	R	S	S	R	S	R	R	1	0	0	1
8-4	S	S	R	S	S	R	S	S	R	0	0	1	1
9-1	R	S	R	R	S	S	S	S	R	1	0	3	4
9-2	R	S	R	R	S	S	S	R	R	1	1	0	2
9-3	R	S	R	R	S	R	S	R	R	1	0	0	1
10-1	R	S	S	R	S	S	S	R	R	1	0	1	2
10-2	R	S	S	R	S	R	R	R	R	0	1	0	1
10-3	R	S	S	R	S	S	R	S	R	0	1	1	2
10-4	R	S	S	R	S	R	S	S	R	0	0	1	1
10-5	R	S	S	R	S	S	S	S	R	0	0	1	1
11-1	S	S	S	R	S	S	S	S	R	2	0	1	3
11-2	S	S	S	R	S	S	S	R	R	4	0	1	5
11-3	S	S	S	R	S	R	S	R	R	1	1	1	3
12-1	S	S	R	R	S	R	S	S	R	1	0	1	2
12-2	S	S	R	R	S	R	R	R	R	1	0	0	1
12-3	S	S	R	R	S	R	S	R	R	1	0	0	1
12-4	S	S	R	R	S	S	S	S	R	0	3	0	3
13-1	S	R	R	S	S	S	S	S	R	0	3	1	4
13-2	S	R	R	S	S	S	S	R	R	2	0	2	4
13-3	S	R	R	S	S	R	S	S	R	0	1	0	1
13-4	S	R	R	S	S	R	R	R	R	0	1	0	1
14-1	R	S	R	S	S	S	S	R	R	1	3	0	4
14-2	R	S	R	S	S	R	S	S	R	0	1	0	1
15-1	S	S	S	S	R	S	S	R	R	1	0	0	1
16-1	S	R	S	R	S	S	S	S	R	0	3	0	3
16-2	S	R	S	R	S	R	S	S	R	0	2	0	2
16-3	S	R	S	R	S	S	S	R	R	0	1	0	1
16-4	S	R	S	R	S	R	S	R	R	0	1	0	1
16-5	S	R	S	R	S	R	R	R	R	0	0	1	1
17-1	R	R	R	S	S	R	S	S	R	0	1	0	1
18-1	R	R	R	R	S	R	R	R	R	0	2	0	2
18-2	R	R	R	R	S	R	S	R	R	0	1	0	1
19-1	R	S	R	R	R	S	R	S	R	0	1	0	1
Total no. of isolates										110	107	82	299

determine whether the virulence situation in *P. hordei* in Israel (2) has reached stability in the process of host-parasite coevolution lasting over millenia (23), or whether new shifts and variations continue to occur.

MATERIALS AND METHODS

Differential hosts. One-leaf seedlings of differential cultivars with specific resistance genes were used in the study. The respective *Pa* designations (6,7,19) and CI numbers are given in parentheses. In order to assess the degree of virulence stability, nine different cultivars employed in previous studies (2) were used: Sudan (*Pa*, CI 6489), Reka 1 (*Pa*2+, CI 5051), Quinn (*Pa*2+*Pa*5, CI 1024), Bolivia (*Pa*2+*Pa*6, CI 1257), Egypt 4 (*Pa*8, CI 6481), Peruvian (*Pa*2, CI 935), Gold (*Pa*4, CI 1145), Estate (*Pa*3, CI 3410), and Cebada Capa (*Pa*7, CI 6193). The first five differentials were described by Levine and Cherewick (11) in the pioneering research on physiologic specialization of *P. hordei*. In 1984 and 1985, three more differential lines were added to test their value in protection against the pathogen: Ricardo (*Pa*2+, CI 6306), Magnif (*Pa*5, CI 13806), and Abyssinian (*Pa*9, CI 1243).

Seed of the differential cultivars was kindly provided by the USDA-ARS, Beltsville, MD, except the seed of Magnif and Abyssinian, which were provided by M. Reinhold, Montana State University, Bozeman.

Isolates. Because cultivated barley (*H. vulgare* L.) occupies a limited acreage in Israel, most of the *P. hordei* isolates were obtained from *H. spontaneum*, the putative progenitor of cultivated barley. *P. hordei* isolates from *H. vulgare* and *H. spontaneum* are cross-compatible (2). Inoculum originating from a single uredium for each isolate was increased on seedlings of the universally susceptible cultivar Nigrate (CI 2444), collected onto glass vials, and preserved at 4 C until inoculation. Due to technical difficulties, we could not sample an adequate number of isolates from *Ornithogalum* plants. Physiologic specialization was determined for 299 isolates (110 in 1983, 107 in 1984, and 82 in 1985) collected from different geographical regions in Israel.

Inoculation. Plants at the single leaf stage were sprayed with a water solution containing 0.05% Tween 20 (polyoxyethylene sorbitan monolaurate). Leaves were inoculated by rubbing with cotton swabs moistened in a water suspension of urediospores. Inoculated plants were maintained in a Percival dew deposition chamber at 18 C, and after 24 hr were transferred to a growth chamber (Karl Weiss, Model 5.5E IU-PK) at 18 C, with 10,000 lx light intensity and 12-hr photoperiods. The infection types were read at 12 and 14 days after inoculation.

Reaction classes. Disease reactions were classified according to Levine and Cherewick (11). Infection types ranging from 0 to 2+ were placed in the resistant class (R); infection types varying from 3– to 4 were placed in the susceptible class (S). Parasitism of the fungus on a specific host may have a phenotype of "virulence" denoted as a susceptible reaction (S), or "avirulence" as expressed by a resistant reaction (R) of the barley plant. A combination of virulence and avirulence toward individual components of the set of differentials constitutes a "virulence pattern" (2,21).

RESULTS

Nineteen virulence patterns were distinguished from reactions elicited on the first five differentials (Table 1) originally used by Levine and Cherewick (11). Sixty-seven patterns were identified with the aid of nine differentials used by Anikster (2) and were employed here in order to compare the virulence situation in Israel during 1983–1985 with that of 1973–1976 (2). Notably, patterns representing the broadest range of virulence, such as 1-1, 1-2, 2-2, and 3-1 include 138 of 299 isolates studied (Table 1). Only isolate 1-5 was virulent on Cebada Capa endowed with gene *Pa*7. Virulence pattern 1-1 is of countrywide distribution, including the arid Negev area.

Studies in Israel with *P. hordei* isolates constituting a broad and diverse spectrum of virulence have suggested the possibility of existence in some differentials of resistance factors previously unknown. For example, the distinction in reaction of Reka 1 (*Pa*2+) and Peruvian (*Pa*2) to isolate 1-6 (Table 1) suggests the presence in the latter differential of a resistance factor or

Table 2. Virulence patterns in *Puccinia hordei* isolates in 1984 and 1985 when three additional differential lines, Ricardo, Magnif, and Abyssinian, are used

Virulence patterns	Ricardo *Pa*2+	Magnif *Pa*5	Abyssinian *Pa*9	No. of isolates		
				1984	1985	Total
1-1-A	S	S	S	8	13	21
1-1-B	S	R	R	4	0	4
1-1-C	S	S	R	4	6	10
1-1-D	R	S	S	1	0	1
1-1-F	R	R	R	1	0	1
1-2-A	S	S	S	1	4	5
1-2-B	S	R	R	5	0	5
1-2-C	S	S	R	10	2	12
1-2-D	R	S	S	1	0	1
1-2-E	S	R	S	1	0	1
1-3-A	S	S	S	1	0	1
1-3-D	R	S	S	0	1	1
1-4-A	S	S	S	1	1	2
1-4-B	S	R	R	0	1	1
1-4-D	R	S	S	0	1	1
1-6-A	S	S	S	1	0	1
1-6-E	S	R	S	0	1	1
1-7-A	S	S	S	1	0	1
1-7-C	S	S	R	1	0	1
2-1-A	S	S	S	2	3	5
2-1-C	S	S	R	1	2	3
2-2-A	S	S	S	1	2	3
2-2-B	S	R	R	1	2	3
2-2-C	S	S	R	3	6	9
2-3-G	R	S	R	0	1	1
2-4-B	S	R	R	0	1	1
3-1-A	S	S	S	3	9	12
3-1-B	S	R	R	1	0	1
3-1-C	S	S	R	2	0	2
3-2-A	S	S	S	5	1	6
3-2-E	S	R	S	0	1	1
3-4-A	S	S	S	1	0	1
4-2-A	S	S	S	1	1	2
4-2-D	R	S	S	1	0	1
4-3-D	R	S	S	1	0	1
4-4-B	S	R	R	1	0	1
4-5-D	R	S	S	0	1	1
5-1-A	S	S	S	0	1	1
5-3-A	S	S	S	0	2	2
5-3-D	R	S	S	2	0	2
5-4-C	S	S	R	0	1	1
6-1-F	R	R	R	1	0	1
6-2-G	R	S	R	1	0	1
6-3-D	R	S	S	1	0	1
6-3-F	R	R	R	1	0	1
6-3-H	R	R	S	1	0	1

(*continued on next page*)

factors absent in Reka 1. Likewise, resistance of Reka 1 to isolates 2-1 or 2-4, both virulent on Peruvian, can indicate the presence in Reka 1 of resistance factors absent in Peruvian. Introduction of three additional differentials (Table 2) enabled better virulence differentiation among isolates belonging to the same virulence pattern. Thus, isolates grouped into a single pattern 1-1 (Table 1) could be subdivided into five different patterns in Table 2. This is true also of the virulence pattern 1-2, 1-3, 1-4, and several others (Table 2).

The protective efficiency of genes and gene combinations against *P. hordei* was assessed by calculating the percentage of avirulence of the tested isolates (Table 3). Gene *Pa*7 in Cebada Capa provides very good protection against nearly all isolates. Gene *Pa*3 in Estate and *Pa*9 in Abyssinian confer resistance to 47.16 and 42.8% of isolates, respectively. The least effective is the gene *Pa*8 in Egypt 4.

DISCUSSION

The barley leaf rust pathogen *P. hordei* is common in Israel on *H. spontaneum* species (1). Both the main and alternate hosts are indigenous to the Mediterranean region. *P. hordei* as an obligate parasite has coevolved for millenia with the hosts. Studies in Israel have corroborated the hypothesis that prolonged host-parasite coexistence results in dual-balanced polymorphism (23). This phenomenon is reflected in genetic diversity of the pathogen population and stability of its composition. For example, *P. coronata* Cda. f. sp. *avenae* F. & L. has coevolved from remote antiquity with the indigenous *Avena* spp. and *Rhamnus* spp. Its populations consist of many physiologic races with remarkably stable composition, as evidenced by consistent predominance of race 276-264 over 30 years of race surveillance (23). In *P. hordei*, Anikster (2) reported prevalence of the same virulence patterns in populations sampled during 1973–1976. We expected similar stability to occur in the ensuing years. Yet, data of studies conducted from 1983 through 1985 disprove this assumption. The two leading patterns of 1983–1985, 1-1 and 1-2 (Table 2), ranked seventh and 12th in order of prevalence during 1973–1976 (2; Table 1). Notably, during 1983–1985, 10.37 and 1% of isolates were avirulent, respectively, on Gold (*Pa*4) and Egypt 4 (*Pa*8), whereas all 1,062 isolates sampled during 1973–1976 from the main and alternate hosts were virulent on both differentials (2).

The contrast between virulence stability in *P. coronata* f. sp. *avenae* and virulence shifts in *P. hordei* can at least partly be ascribed to the decline of the gametophytic stage in the crown rust fungus as compared with the vigorous activity of that stage in *P. hordei* (23). Conceivably, the process of regressive evolution associated with weakening of the gametophytic stage that takes place in heteroecious rust fungi under adverse ecologic conditions (4) in regions with rainless summers will gradually reduce the significance of that stage in *P. hordei* and its ability to change the virulence picture.

Khokhlova (10) analyzed the parasitic specialization of *P. hordei* collected in the USSR in regions that were far apart. Unlike in Israel, virulence in the USSR was uniform. All differentials, except those carrying genes *Pa*3 and *Pa*7, were susceptible. The heterogeneity of virulence in Israel can be attributed to the dynamic role of the sexual stage in generating the variability of *P. hordei*.

Table 2. *(continued from preceding page)*

Virulence patterns	Ricardo *Pa*2+	Magnif *Pa*5	Abyssinian *Pa*9	No. of isolates 1984	1985	Total
6-4-B	S	R	R	1	0	1
6-5-F	R	R	R	0	1	1
8-1-C	S	S	R	1	0	1
8-1-E	S	R	S	0	1	1
8-2-A	S	S	S	1	0	1
8-2-B	S	R	R	3	0	3
8-2-C	S	S	R	1	0	1
8-4-A	S	S	S	0	1	1
9-1-A	S	S	S	0	3	3
9-2-B	S	R	R	1	0	1
10-1-A	S	S	S	0	1	1
10-2-D	R	S	S	1	0	1
10-3-A	S	S	S	1	0	1
10-3-C	S	S	R	0	1	1
10-4-D	R	S	S	0	1	1
10-5-A	S	S	S	0	1	1
11-1-C	S	S	R	0	1	1
11-2-A	S	S	S	0	1	1
11-3-D	R	S	S	0	1	1
11-3-E	S	R	S	1	0	1
12-1-H	R	R	S	0	1	1
12-4-A	S	S	S	1	0	1
12-4-E	S	R	S	2	0	2
13-1-C	S	S	R	0	1	1
13-1-E	S	R	S	0	1	1
13-2-A	S	S	S	1	0	1
13-2-B	S	R	R	1	0	1
13-2-C	S	S	R	0	1	1
13-2-E	S	R	S	1	0	1
13-3-A	S	S	S	1	0	1
13-4-E	S	R	S	1	0	1
14-1-B	S	R	R	1	0	1
14-1-C	S	S	R	1	0	1
14-1 D	R	S	S	1	0	1
14-2-H	R	R	S	1	0	1
16-1-B	S	R	R	1	0	1
16-1-C	S	S	R	2	0	2
16-2-D	R	S	S	1	0	1
16-2-E	S	R	S	1	0	1
16-3-D	R	S	S	1	0	1
16-4-D	R	S	S	1	0	1
16-5-H	R	R	S	0	1	1
17-1-C	S	S	R	1	0	1
18-1-G	R	S	R	2	0	2
18-2-A	S	S	S	1	0	1
19-1-G	R	S	R	1	0	1
Total no. of isolates				107	82	189

Table 3. Percentage of isolates of *Puccinia hordei* avirulent on the single gene differential lines or lines with gene combinations used in the survey from 1983 through 1985

Lines[a]	*Pa* gene	Percentage of avirulent isolates
Sudan*	*Pa*	26.42
Reka 1*	*Pa*2+	26.09
Quinn*	*Pa*2+ *Pa*5	20.07
Bolivia*	*Pa*2+ *Pa*6	20.07
Egypt 4*	*Pa*8	1.00
Peruvian*	*Pa*2	15.38
Gold*	*Pa*4	10.37
Estate*	*Pa*3	47.16
Cebada Capa*	*Pa*7	99.16
Ricardo**	*Pa*2+	16.40
Magnif**	*Pa*5	22.20
Abyssinian**	*Pa*9	42.80

[a] * = Lines tested 3 years with a total of 299 isolates, ** = lines tested in 1984 and 1985 with a total of 189 isolates.

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