

Parasitic Specialization of *Puccinia hordei* in Israel

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ABSTRACT

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Alternate host *Ornithogalum* spp. are important in the perennation of *Puccinia hordei* in Israel. The racial identity of 615 isolates from *Hordeum spontaneum* and 447 isolates from plants of *Ornithogalum* spp. was determined. The isolates were collected from plants growing in the wild in six regions during 3-4 yr in succession. The results suggest that isolates from the alternate host were parasitically more diverse than those from the main host. Populations from both sources had 17 virulence patterns in common;

five patterns were present only on the alternate host and one was limited to the main host. Some virulence patterns were particularly common each year in all regions. A number of isolates from the main and alternate host rendered ineffective all known genes for specific resistance including *Pa7* (in cultivar Cebada Capa), *Pa3* (in cultivar Estate), and *Pa9* (in USDA CI 1243).

Barley is of great importance in world food production, ranking fourth among cereals (23). It is one of the most reliable cereals where drought, short growing season, and alkaline soil are encountered. Large human populations depend on barley in India and China and in the Mediterranean, Middle Eastern and Andean regions (5).

The brown leaf rust disease caused on barley by *Puccinia hordei* Otth has become important in Europe, Africa, and the Middle East (2). Its presence was reported in 11 countries of the Near East, and in some of them, particularly Egypt, it frequently causes severe losses (1).

Breeding for resistance is recommended for control of this disease (14). Researchers in various countries have studied the parasitic specialization of *P. hordei*, "in order that breeding programmes could proceed logically" (6). Differential cultivars employed in such studies are endowed with major genes conditioning specific resistance. They were reviewed by Clifford (6,7), Golan et al (11), Parlevliet (16), and Rintelen (19).

In 1914, Tranzschel (25) identified several *Ornithogalum* spp. as alternate hosts of *P. hordei* and indicated their importance in intensifying epidemics of brown leaf rust in barley-growing areas. The role of *Ornithogalum* spp. as an alternate host has been confirmed in the USA and some European countries (8,10). Critopoulos (8) demonstrated the significance of the alternate host in the perennation of *P. hordei* in Greece. The results of studies by Z. K. Gerechter-Amitai (*unpublished*) and Anikster et al (3,4) prove that indigenous *Ornithogalum* spp. play an important role in the completion of the life cycle of *P. hordei* in Israel where barley plants normally desiccate during the rainless summer.

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This report summarizes the results of investigations on the parasitic specialization of *P. hordei* on *Hordeum spontaneum* C. Koch, (which grows throughout Israel and is the putative progenitor of cultivated barley) and on alternate *Ornithogalum* spp. hosts. Some of these data have already been published (3,4,11).

MATERIALS AND METHODS

Differential hosts. Single-leaf-stage barley seedling differentials with specific resistance genes (the *Pa* designations of Clifford [6,7] and USDA CI numbers are given below in parentheses) were of the following cultivars: Speciale (*Pa*, CI 7536), Sudan (*Pa*, CI 6489), Reka 1 (*Pa2*, CI 5051), Quinn (*Pa2* + *Pa5*, CI 1024), Bolivia (*Pa2* + *Pa6*, CI 1257), Estate (*Pa3*, CI 3410), Gold (*Pa4*, CI 1145), Cebada Capa (*Pa7*, CI 6193), and Egypt 4 (*Pa8*, CI 6481). Seeds of these cultivars were kindly provided by the USDA, ARS, Beltsville, MD.

Inoculum. In Israel, *P. hordei* parasitizes cultivated barley (*Hordeum vulgare* L.), *H. spontaneum*, *H. bulbosum* L., and *H. murinum* L. (4). *P. hordei* isolates from *H. vulgare* and *H. spontaneum* are cross-compatible. They alternate with *Ornithogalum brachystachys* C. Koch, *O. eigii* Feinbr., and *O. trichophyllum* Boiss, et Heldr. (2).

Since barley is cultivated in Israel only on a limited scale, the isolates of *P. hordei* that were investigated were isolated from *H. spontaneum* and the alternate hosts *O. brachystachys* and *O. eigii*. Parasitic specialization was determined for 615 uredial isolates and 447 aecial isolates. From 1973 through 1976 in Upper Galilee, Lower Galilee, the Judean foothills, and the southern coastal plain: 81, 95, 172, and 166 isolates, respectively, were collected from *H. spontaneum* and 76, 55, 135, and 81 isolates, respectively, were collected from *Ornithogalum* species. In addition, from 1974 to 1976, 46 uredial and 32 aecial isolates were collected in the Judean Mountains and 55 uredial and 68 aecial isolates were collected in the Samaritan foothills.

Inoculation. Inoculum was multiplied on seedlings of the universally susceptible cultivar Nigrate (CI 2444). Most isolates subsequently identified were of monouredial or single aecial cluster origin. Leaves were inoculated by gently rubbing with cotton swabs

moistened in a urediospore suspension. Prior to inoculation seedlings were sprayed with 0.05% water solution of Tween-20 (polyoxyethylene sorbitan monolaurate). The inoculated seedlings were maintained for 24 hr in water-saturated atmospheres in growth chambers maintained at 19–21 C and then placed on greenhouse benches at the same temperature. Readings of the developed pustules were made twice, 10 and 14 days after inoculation. The reactions were classified according to Levine and Cherewick (12). 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).

In this paper, the term "parasitism" designates a trait of the fungus. On a specific host this character may have a phenotype of "virulence" denoted by susceptible reaction (S), or "avirulence" as expressed by resistant reaction (R) of the barley plant. The combination of virulence and avirulence toward individual components of the set of differentials constitutes a "virulence pattern" (22).

RESULTS

Virulence of isolates isolated from the main and alternate hosts.

The overall pathogenicity of 615 cultures from *H. spontaneum* and 447 cultures from *Ornithogalum* spp. collected countrywide annually from 1973 through 1976 is shown in Table 1. The data reveal great similarity in the parasitism of *P. hordei* obtained from these two sources. They have in common 17 virulence patterns representing 940 cultures. Some cultures derived from both hosts were virulent on accessions which in combination possess all the presently recognized genes for resistance, including gene *Pa7* in cultivar Cebada Capa (virulence pattern 16). Gene *Pa7* reportedly offers resistance to *P. hordei* worldwide, except in Morocco (17). Cultures from Morocco are virulent on cultivar Cebada Capa but avirulent on accessions endowed with the gene *Pa9* (17), while cultures from Israel develop uredia of infection type 3 on seedlings of the accession CI 1243 carrying the gene *Pa9* (unpublished). Notably, over 81% of isolates listed in Table 1 were virulent on cultivar Estate which possesses gene *Pa3*, offering protection against most isolates of *P. hordei* elsewhere (16,18,24). Five

TABLE 1. Virulence patterns in 615 isolates of *Puccinia hordei* from plants of *Hordeum spontaneum* and 447 isolates from plants of *Ornithogalum* spp.

Virulence pattern number	Virulence patterns on differential cultivars: ^a										No. of isolates representing each pattern
	Speciale (<i>Pa</i>)	Sudan (<i>Pa</i>)	Reka 1 (<i>Pa2</i>)	Quinn (<i>Pa2</i> + <i>Pa5</i>)	Bolivia (<i>Pa2</i> + <i>Pa6</i>)	Estate (<i>Pa3</i>)	Gold (<i>Pa4</i>)	Cebada Capa (<i>Pa7</i>)	Egypt 4 (<i>Pa8</i>)		
1 ^c	S ^b	R	R	R	R	S	S	R	S	136	
2 ^c	R	R	R	R	R	R	S	R	S	132	
3 ^c	S	S	R	R	R	R	S	R	S	131	
4 ^c	S	S	R	S	S	S	S	R	S	110	
5 ^c	S	S	R	R	R	S	S	R	S	87	
6 ^c	S	S	S	R	R	S	S	R	S	77	
7 ^c	S	S	S	S	S	S	S	R	S	51	
8 ^c	R	R	S	S	S	S	S	R	S	47	
9 ^c	S	S	S	S	R	S	S	R	S	37	
10 ^c	R	R	S	R	R	S	S	R	S	36	
11 ^c	S	R	S	R	R	S	S	R	S	31	
12 ^c	S	S	S	S	S	R	S	R	S	31	
13 ^c	R	R	R	R	R	R	S	R	S	18	
14 ^c	S	S	R	S	R	S	S	R	S	11	
15 ^c	S	S	R	R	R	S	S	S	S	3	
16 ^c	S	S	S	S	S	S	S	S	S	2	
17 ^c	S	S	S	R	R	S	S	S	S	2	
18 ^d	S	R	S	R	S	S	S	R	S	24	
19 ^d	S	R	S	S	R	S	S	R	S	21	
20 ^d	S	S	R	R	S	R	S	R	S	19	
21 ^d	R	R	S	S	R	S	S	R	S	18	
22 ^d	S	S	R	R	S	S	S	R	S	17	
23 ^e	R	R	S	R	S	S	S	R	S	23	

^a Resistance gene complements as designated by Clifford (6,7) are given in parentheses.

^b R = resistant and S = susceptible.

^c Virulence patterns common to cultures isolated from plants of both *Hordeum spontaneum* and *Ornithogalum* spp.

^d Virulence patterns of isolates from plants of *Ornithogalum* spp. only.

^e Virulence patterns of isolates from plants of *Hordeum spontaneum* only.

virulence patterns comprising 99 isolates were identified only in aeciospore progenies while only one virulence pattern (pattern 23) was restricted to isolates derived from *H. spontaneum*. Similarity of reactions induced by a number of cultures of *P. hordei* on cultivars Speciale and Sudan led to the conclusion that both are protected by the same gene *Pa* (13). Tests in Israel with isolates constituting a broader range of parasitism revealed distinction in the reactions of cultivars Speciale and Sudan to some isolates from *H. spontaneum* and *Ornithogalum* species. Such differences suggest that cultivar Sudan has a gene or genes other than *Pa* (Table 1, virulence patterns 1, 11, 18, and 19). This contention is supported by evidence provided by Moseman (13). Resistance of Reka 1 to isolates virulent on accessions combining *Pa2* + *Pa5* or *Pa2* + *Pa6* (virulence patterns 4, 14, 20, and 22) corroborates the assumption that Reka 1 has, in addition to gene *Pa2*, another gene or other genes for resistance (18,24).

Cultures of *P. hordei* of aeciospore origin from Lower Galilee and the Judean and Samarian foothills were more diversified and comprised more virulence patterns than those isolated from *H. spontaneum*. The reverse was true of the respective cultures in the Upper Galilee, while in the Judean mountains and the southern coastal plain, the range of parasitism was similar. Several virulence patterns were particularly common and appeared in successive years in populations secured from the main and alternate host. This was true in the first place of the patterns with components avirulent on cultivars Reka 1, Quinn, Bolivia, and Cebada Capa (Table 1, virulence patterns 1, 2, 3, 5). The cultures concerned amounted to about 45.7% of the total number of isolates.

Analysis of data in Table 1 suggests that isolates of *P. hordei* from *Ornithogalum* spp. are parasitically more diverse than those from *H. spontaneum*. Among 447 isolates of aecial origin, there were 22 virulence patterns versus 18 virulence patterns among 615 isolates from the main host. Furthermore, the five virulence patterns (patterns 18–22 in Table 1) restricted to plants of *Ornithogalum* spp., comprised 99 isolates, 9.3% of the total secured from this source. In contrast, virulence pattern 23, which was limited to *H. spontaneum*, comprised 23 isolates, 2.1% of isolates collected on the main host.

Effect of alternate host on parasitic variability of the fungus. To assess the influence of the functioning alternate host on the parasitic diversity of *P. hordei*, 25 urediospore isolates were randomly collected from *H. spontaneum* in two locations in the neighborhood of rusted plants of *Ornithogalum* spp., and the same number of isolates was procured from two locations where the alternate host could not be found <300 m from the plants of *H. spontaneum* that were investigated. In all places the fungus developed profusely on *H. spontaneum*. Since both tests showed similar trends, only results of one of them are presented (Table 2). Data assembled horizontally demonstrate that five virulence patterns were present in populations isolated from the vicinity of

plants of *Ornithogalum* spp., while in locations free of *Ornithogalum* spp. uredial populations were comprised of only three virulence patterns. Results arranged vertically reveal a similar situation. In uredial populations collected in the proximity of the alternate host six resistance:susceptibility (R:S) combinations were found, while in populations from places devoid of *Ornithogalum* spp. the data revealed only four combinations. These results also suggest that isolates of *P. hordei* from the alternate host are parasitically more specialized than those derived from *H. spontaneum*.

DISCUSSION

Israel is a part of the common center of origin and genetic variation of *H. spontaneum* and a number of *Ornithogalum* spp. Populations of *H. spontaneum* are genetically very diverse (15). *P. hordei* thrives abundantly on this wild barley and completes the alternate generation of its life cycle on plants of a number of *Ornithogalum* species (2).

The alternate host is important in the perennation of the fungus. According to D'Oliveira (9,10), *H. spontaneum*, *Ornithogalum* spp., and *P. hordei* in the Mediterranean region have undergone a long coevolution which has resulted in balanced polymorphism of the components in the host-parasite system (4). Consequently, populations of *P. hordei* constitute a broad spectrum of parasitic diversity. The genetic diversity of *H. spontaneum* provides numerous niches that expedite the establishment of many parasitic strains originating on the alternate host by hybridization and genetic recombination of the fungus. The data attest to a broad array of parasitic variation in populations of *P. hordei* derived from the main and alternate host. The patterns of virulence detected in studies of cultures procured from *H. spontaneum* and *Ornithogalum* spp. during 1973–1976, were similar. Virulence patterns identified among isolates produced by the gametophytic as well as the sporophytic stage of *P. hordei* render ineffective resistance carried by all tested differentials. Significantly, natural communities of plants of *H. spontaneum* and *Ornithogalum* spp. are well buffered against the parasite by different types of protection (21). Populations of *P. hordei* originating from aecia seem to be more pathogenically diverse than uredial populations derived from *H. spontaneum*. For example, they embraced five of 23 virulence patterns (Table 1, virulence patterns 18–22) which were not found among fungus populations originated from the main host. Also uredial populations sampled on a limited scale from *H. spontaneum* in the vicinity of the alternate host appeared to be somewhat more diversified than those collected on wild barley distant from plants of *Ornithogalum* spp. (Table 2).

In the broad spectrum of parasitic variability some virulence patterns were common on the main and alternate host in all regions

TABLE 2. Virulence patterns of 25 isolates of *Puccinia hordei* randomly sampled on *Hordeum spontaneum* plants near rusted alternate host *Ornithogalum* spp. plants at Nahshon-Judean foothills, and of 25 cultures sampled from *H. spontaneum* distant from the alternate host in the Latrun-Judean foothills

Loc ^a	Seedling reactions of the differential barley cultivars:								R/S ratio ^b
	Cebada Capa (Pa7)	Bolivia (Pa2 + Pa6)	Quinn (Pa2 + Pa5)	Reka 1 (Pa2)	Estate (Pa3)	Sudan (Pa)	Gold (Pa4)	Egypt 4 (Pa8)	
A	R	R	R	R	S	S	S	S	4/4 (5)
	R	R	R	R	R	R	S	S	6/2 (1)
	R	R	R	R	R	S	S	S	5/3 (7)
	R	R	S	S	S	S	S	S	2/6 (2)
	R	S	S	S	S	S	S	S	1/7 (10)
R:S	5/0	4/1	3/2	3/2	2/3	1/4	0/5	0/5	Total: 5 R:S ratios
B	R	R	R	R	R	S	S	S	5/3 (16)
	R	S	R	S	R	S	S	S	3/5 (3)
	R	S	S	S	S	S	S	S	1/7 (6)
R:S	3/0	1/2	2/1	1/2	1/2	0/3	0/3	0/3	Total: 3 R:S ratios

^aLocations: A = isolates collected from *H. spontaneum* near the alternate host; B = isolates collected from *H. spontaneum* far from the alternate host.

^bFigures in parentheses indicate the number of isolates represented in the respective R:S ratio.

concerned. Possibly, such virulence patterns are associated with genes for preferential survivability (20).

The populations of *P. hordei* that were investigated have some outstanding features, like the prevalence of virulence on cultivar Estate, which possesses gene *Pa3*. This gene is effective against *P. hordei* in a number of countries. Virulence on Cebada Capa was discovered first in Israel, initially in isolates from plants of *Ornithogalum* spp. (11) and thereafter in isolates from *H. spontaneum* (4).

The prediction that virulence on cultivar Cebada Capa constitutes a potential threat to barley crops in other countries (11), was substantiated by the discovery in Morocco of cultures of *P. hordei* that were virulent on this cultivar (17). This finding is of practical importance since gene *Pa7* from Cebada Capa is being incorporated by breeders into commercial cultivars (17).

Obviously, studies of parasitism in fungi in their centers of origin and evolution can shed light on their potential virulence and indicate what can be expected in other countries where the host crops are grown (26). In the case of heteroecious fungi, such studies should be conducted where the centers of evolution of the gametophytic and sporophytic generations coincide (9,10).

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