

Alternate Hosts of *Puccinia hordei*

Y. Anikster

Senior lecturer, Faculty of Life Sciences, Tel-Aviv University, Tel-Aviv, Israel 69978.

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ABSTRACT

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Accessions of native Liliaceae species, *Ornithogalum brachystachys*, *O. trichophyllum*, *Dipcadi erythraeum*, and *Leopoldia eburnea* support formation of pycnia and aecia of *Puccinia hordei* when inoculated with cultures isolated from cultivated barley or each of the native wild barleys, *Hordeum spontaneum*, *H. bulbosum*, and *H. murinum*. Solitary pycnia on each of the alternate hosts produced aecia when intermixed with nectar from another pycnium formed on any one of the mentioned Liliaceae species. Aeciospores infected only the *Hordeum* species that was the source

of teliospores for inoculation of the alternate host, except that reciprocal inoculations of *H. spontaneum* and *H. vulgare* were successful. In contrast, regardless of their origin, the monokaryotic stages are pathogenically less specialized and have common host in *O. brachystachys*, *O. trichophyllum*, *D. erythraeum*, and *L. eburnea*. Rust cultures from each of the alternate hosts inoculated with a common collection of teliospores, showed similar spectra of virulence on seedlings of *H. vulgare* endowed with different specific genes for resistance to brown leaf rust.

Tranzschel (15,16) proved that some *Ornithogalum* species are alternate hosts of *Puccinia hordei* Otth., the incitant of brown leaf rust on barley. The alternate host increases the disease severity in several regions of the USSR (15,16) and promotes evolution of rust strains characterized by abundant teliospore production (15). Research in the USA (11) and Europe (3,5,14) reaffirmed the role of *Ornithogalum* as the alternate host of *P. hordei*. The alternate host is of decisive importance for the perpetuation of the fungus in the

Mediterranean region where *Hordeum* plants do not survive the rainless summer (3). D'Oliveira's (14) studies in Portugal have demonstrated that *P. hordei* is compatible with the indigenous *Ornithogalum* species, but not with species originating in other parts of the world. However, in greenhouse tests in Portugal (12), *P. hordei* produced pycnia and aecia on *Dipcadi serotinum* (L.) Medic., which serves as alternate host of the fungus in natural habitats of Kenya (8).

Israel is located in one of the centers of origin and genetic diversification of several species of *Hordeum* and the family Liliaceae. In that region, fungi obligately parasitic on indigenous wild barleys, possess a wider host range, as a result of protracted host-parasite coevolution, than fungi of the same species have in other regions (2).

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Puccinia hordei has coevolved in Israel with plants of native *Hordeum* spp. and other species of the Liliaceae (2). The purpose of this study was to explore the host range of the monokaryotic generation of *P. hordei* on endemic species of Liliaceae.

MATERIALS AND METHODS

Inoculum. Leaves of *Hordeum spontaneum* C. Koch, *H. bulbosum* L., and *H. murinum* L. covered with telia of *P. hordei* were subjected to the treatment for stimulating teliospore germination designed by Anikster (10). Then, wet 0.5- to 1.0-cm-long leaf segments bearing telia were placed on leaves of the Liliaceae plants being investigated. The tested plants were grown from bulbs collected in nature and planted in 15-cm-diameter clay pots filled with garden soil. The intact inoculated leaves were enclosed in glass or polyethylene cylinders topped with moist cheesecloth pads, and maintained in a greenhouse at about 20 ± 2 C. The pads were removed 24 hr after inoculation. The aeciospores formed were inoculated to seedlings of the standard susceptible barley cultivar Nigrate (CI 2444). Copious urediospore production was obtained.

Virulence of the rust fungus was determined by inoculating urediospores to seedlings of barley cultivars endowed with specific genes for resistance to *P. hordei* (6).

Liliaceae plants. Search for the alternate host was conducted among the following indigenous wild plants of Liliaceae subfamily Lilioideae: *Ornithogalum brachystachys* C. Koch, *O. trichophyllum* Boiss. et Heldr.; *Dipcadi erythraeum* Webb et Bert.; *Bellevalia desertorum* Eig et Feinbr., *B. eigii* Feinbr., *B. flexuosa* Boiss., *B. macrobotrys* Boiss., *B. stepporum* Feinbr., *B. zoharyi* Feinbr.; *Leopoldia comosa* (L.) Parl., *L. eburnea* Eig et Feinbr., *L. longipes* (Boiss.) A. Los., *L. maritima* (Desf.) Parl.; *Scilla autumnalis* L., *S. hanburyi* Bak.; *S. hyacinthoides* L.; *Urginea undulata* (Desf.) Steinh.

The taxonomic identity of the Liliaceae and *Hordeum* plants was determined with the aid of the analytical key by Eig et al (4). The genera, *Bellevalia*, *Leopoldia*, *Scilla*, and *Urginea* were chosen since some of their components are compatible with macrocyclic and microcyclic *Uromyces* species related to *P. hordei* (2).

RESULTS

Alternate hosts. Pycnia and aecia formed on *O. brachystachys*, *O. trichophyllum*, *D. erythraeum*, and *L. eburnea* when these plants were exposed to germinating teliospores of *P. hordei* produced on *H. spontaneum*, *H. bulbosum* and *H. murinum*, but they did not form on other tested taxa of Liliaceae (Table 1).

Aecia developed readily from crowded pycnia, whereas solitary pycnia gave rise to aecia only when nectar from other pycnia was applied to them. Aecia also were produced from pycnia on *D. erythraeum* or *L. eburnea* after application of nectar from *O. brachystachys*. Likewise, solitary pycnia on the latter host

developed aecia when fertilized with nectar produced on *D. erythraeum* or *L. eburnea*. Aeciospores derived from cultures from *H. vulgare*, *H. spontaneum*, *H. bulbosum*, or *H. murinum* were compatible only with plants of the respective source species from which the teliospores were obtained, except that aeciospores produced by cultures originating from *H. vulgare* and *H. spontaneum* were infectious on accessions of both species. In limited tests made so far, teliospores formed on cultivated barley as a result of inoculation with aeciospores isolated from *O. brachystachys*, *D. erythraeum* and *L. eburnea*, induced infections leading to production of aecia when reinoculated to the Liliaceae source hosts.

Both *D. erythraeum* and *L. eburnea* are restricted in distribution to the desert areas of Israel, which are virtually free of *P. hordei*. However, accessions of the two species, emerging from bulbs planted by us in relatively humid regions, became infected by the parasite as a result of natural inoculation (Table 2). Wild barleys are regularly stricken by leaf rust in those relatively humid locations.

Parasitic specialization. Foliage of *O. brachystachys*, *D. erythraeum*, and *L. eburnea* was exposed to germinating teliospores of *P. hordei* formed on leaves of *H. spontaneum* in Judean Foothills. Aeciospores that developed on the three species were inoculated separately to seedlings of Nigrate. Single spore isolates derived from uredia were then increased individually on seedlings of Nigrate and their progenies inoculated to seedlings of *H. vulgare* endowed with specific genes for resistance to *P. hordei* (6). The results (Table 3) attest to similarity of the three sets of cultures. All cultures were virulent on Estate (Pa3), which is generally resistant to *P. hordei* abroad, but very susceptible to most cultures of *P. hordei* isolated in Israel from *Hordeum* and *Ornithogalum* (unpublished).

DISCUSSION

Leaf rust caused by *P. hordei* has become an important barley disease in Europe (6), in Africa and the Middle East (E. L. Sharp, personal communication). Its presence was reported in 11 countries of the Near East (1), and in some of them (eg, Egypt), it causes frequent and severe losses. Since barley leaf rust is widespread in geographic regions with rainless summers, the elucidation of the perennation of the parasitic fungus is of great importance. Critopoulos (3) emphasized the significance of the alternate host *Ornithogalum umbellatum* in the perpetuation of the parasite in Greece (Attica). Studies in Portugal (13) and Israel (2) lead to the conclusion that inoculum generated on the alternate host has a "real significance...to start new epidemics, and as a means of breeding new physiologic races" (13). New, very virulent races were discovered in Israel first among aeciospores and then in urediospores (2,6).

Israel is located in the geographic region where the centers of origin and genetic diversification of native *Hordeum* species and Liliaceae coincide. Oliveira (13) has shown that in heteroecious rust

TABLE 1. Compatibility between Liliaceae species and four groups of *Puccinia hordei* cultures from *Hordeum spontaneum*, *H. bulbosum* and *H. murinum*. Greenhouse tests at 20 ± 2 C

Inoculum ^a	Infected plants/total number of plants of species inoculated						
	<i>Ornithogalum brachystachys</i>	<i>Ornithogalum trichophyllum</i>	<i>Bellevalia</i> spp. ^b	<i>Dipcadi erythraeum</i>	<i>Leopoldia eburnea</i> ^c	<i>Scilla</i> spp. ^d	<i>Urginea undulata</i>
Group A	20/20 ^e	20/20	0/20	20/20	20/20	0/20	0/20
Group B	20/20	17/20	0/20	20/20	16/20	0/20	0/20 ^f
Group C	8/20	6/20	0/20	9/20	12/20	0/20	0/20
Group D	4/4	4/4	0/4	4/4	3/4	0/4	0/4

^a Group A—15 cultures from teliospores on *Hordeum spontaneum* collected throughout Israel; Group B—15 cultures from teliospores on *H. bulbosum* collected throughout Israel; Group C—two cultures collected from two regions of Israel; and Group D—four cultures from single urediospores produced on *H. spontaneum*.

^b *Bellevalia desertorum*, *B. eigii*, *B. flexuosa*, *B. macrobotrys*, *B. stepporum*, and *B. zoharyi*.

^c Incompatible were plants of *Leopoldia comosa*, *L. longipes*, and *L. maritima*.

^d *Scilla autumnalis*, *S. hanburyi*, and *S. hyacinthoides*.

^e Numerator indicates the number of cultures inducing formation of pycnia and aecia; denominator denotes the total number of cultures used for inoculation.

^f Few abortive pycnia formed.

fungi, compatibility with the main and alternate hosts does exist only when both hosts "belong to the same center of origin." The relevance of these findings to *P. hordei* was demonstrated in Israel, where new alternate hosts of the parasite were identified in native *Ornithogalum* species, *D. erythraeum*, and *L. eburnea*. In cultures isolated, respectively, from *H. spontaneum*, *H. bulbosum*, and *H. murinum* congeniality of the dikaryotic stage was confined to plants of the source host species. In contrast, their monokaryons have common hosts in *Ornithogalum* species, *D. erythraeum*, and *L. eburnea*. The data concur with Green's (7) contention that monokaryons are less specialized on the alternate hosts than the dikaryons on the main hosts. Besides, *D. erythraeum* and *L. eburnea* are restricted in distribution to dry regions with very weak incidence of *P. hordei*. Presumably, also the lack of strong preferential selection pressure contributes to the congeniality of the alternate hosts to the tested rust cultures (2).

Of special interest is the compatibility of *L. eburnea* with macrocyclic and microcyclic *Uromyces* species living on Liliaceae (2). These data may indicate phylogenetic relationships between *P. hordei* and the mentioned *Uromyces* spp., and open up new possibilities for the study of their genetics.

TABLE 2. Alternate hosts of *Puccinia hordei* identified in natural inoculation tests^a

Test locations	Tested plants		
	<i>Ornithogalum brachystachys</i>	<i>Dipcadi erythraeum</i>	<i>Leopoldia eburnea</i>
Bet-Meir (Judean Mountains)	6/8 ^b	3/8	1/8
Shaar HaGay (Judean Foothills)	6/8	2/8	3/8

^aPotted plants of listed Liliaceae species were maintained in natural habitats at the two listed locations.

^bNumerator indicates number of plants on which pycnia and aecia were formed; denominator denotes the total number of tested plants in the respective species.

TABLE 3. Rust reactions on differential barley cultivars inoculated with single urediospore cultures of *Puccinia hordei* derived from aeciospores produced on three Liliaceae species following inoculation with teliospores from naturally inoculated *Hordeum spontaneum*

Inoculated cultivars	Resistance genes	Sources of aeciospores inoculum		
		<i>Ornithogalum brachystachys</i>	<i>Dipcadi erythraeum</i>	<i>Leopoldia eburnea</i>
Sudan (CI 6489)	Pa	S S S	S S S	S S S
Bolivia (CI 1257)	Pa2+Pa6	S R R	S R R	S R R
Quinn (CI 1024)	Pa2+Pa5	S S R	S S R	S S R
Reka I (CI 5051)	Pa2	S R R	S R R	S R R
Gold (CI 1145)	Pa4	S S S	S S S	S S S
Estate (CI 3410)	Pa3	S S S	S S S	S S S
Cebada Capa (CI 6193)	Pa7	R R R	R R R	R R R
		4 ^a 5 2	5 5 1	6 4 1

^aNumbers of isolates that induced the listed reaction spectra on the sets of inoculated seedlings.

The expansion of the rust from the primary to secondary hosts, labeled "biogenic radiation," by Leppik (9), proceeds in the heteroecious rust fungi by moving either the monokaryotic or the dikaryotic generation to the new host (2). In *Uromyces* species on *Hordeum* native in Israel, expansion of the parasite seems to take place by increasing the range of aecial host genera, like *Bellevalia*, *Muscari*, and *Scilla* (2). Similar trends have probably developed in *P. hordei* with the sporophytic generation on barley and aecia on *Ornithogalum*, *Dipcadi* and *Leopoldia*. More research is in progress to elucidate this relationship.

Gäumann (5) stipulated that an experimental proof of alternation of brown leaf rust isolates from *H. murinum* with *Ornithogalum* plants would be the "experimentum crucis" justifying their classification as *P. hordei*. Obviously, our studies have provided such evidence.

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