Host Range of *Pyrenophora teres* f. *teres* Isolates from California

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ABSTRACT

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The host range of *Pyrenophora teres* f. *teres* (net blotch pathogen of barley) isolates from California was studied in the growth chamber and in the field. In the growth chamber, 28 of 43 gramineous species tested were infected by at least one of six *P. t. teres* isolates originating from *Hordeum vulgare* or *H. murinum* subsp. *leporinum*. Sixty-five of 95 species evaluated in the field also were infected, and 38 new host species were identified. On a generic basis, 15 of the 16 genera tested had susceptible species; this list included four genera (*Cynodon, Deschampsia, Hordelymus,* and *Stipa*) never reported to contain hosts for *P. t. teres*. Among the wild grasses tested, only *H. m. leporinum* consistently exhibited the netted lesions characteristic of infection by virulent isolates of *P. t. teres* on susceptible genotypes of *H. vulgare*. However, an isolate of the pathogen collected from *H. m. leporinum* exhibited reduced virulence on barley cultivars and may represent pathogenic specialization to the wild host. The net blotch fungus was reisolated from all species infected in the field trial, and these isolates retained their pathogenicity on barley after a single passage through alternative hosts. The broad host range of *P. t. teres* under field conditions indicates the potential of alternative hosts as sources of primary inoculum; however, their role in actually initiating epidemics of net blotch in California is still unresolved.

Net blotch, an important disease of barley (*Hordeum vulgare* L.) in many cereal-growing regions of the world, is caused by the fungus *Pyrenophora teres* Drechs. f. *teres* Smedeg. (anamorph: *Drechslera teres* (Sacc.) Shoemaker f. *teres* Smedeg.). The disease is common on barley in California and under favorable environmental conditions can cause complete leaf necrosis on susceptible cultivars by the flowering stage of plant development (20). Yield losses exceeding 35% were reported for the susceptible cultivar Kombar in field trials at Davis, California (23).

The primary inoculum of *P. t. teres* commonly originates from infected plant debris (8,11) and seed (8,16). However, wild grass species may also be a potential source of primary inoculum, as indicated by the 47 species in 18 genera of the Poaceae that have been infected by *P. t. teres* in artificial inoculation studies (21). In Israel, natural infection by *P. t. teres* is restricted to species in the genus *Hordeum* (12). Cross-inoculation experiments have shown that isolates from *H. murinum* L., *H. murinum* subsp. *leporinum* (Link) Arcang., *H. marinum* Huds., and *H. vulgare* subsp. *spontaneum* (C. Koch) Thell. are capable of infecting both cultivated barley (12) and all of the other respective wild *Hordeum* species tested (11). Kenneth et al (13) considered *H. v. spontaneum* to be an epidemiologically significant host for net blotch in Israel because it is indigenous to the area and is capable of harboring different pathotypes of *P. t. teres*. In Western Australia, *P. t. teres* has been isolated from *Hordeum* species and from *Bromus diandrus* Roth (Syn. *B. gussonii* Parl.) (15). Isolates of *P. t. teres* from *B. diandrus* and *H. marinum* subsp. *gussoneanum* (Parl.) Thell. (Syn. *H. geniculatum* All. and *H. hystrix* Roth) were able to infect cultivars of *H. vulgare* (15); however, isolates from *H. m. leporinum* and *H. vulgare* were unable to cross-infect and exhibited host specialization (14). In California, natural infections by *P. t. teres* have been observed on *H. vulgare* and the *H. murinum* subspecies *leporinum* and *glaucum* (Steud.) Tzvelev (17; M. P. Brown and B. J. Steffenson, *unpublished*). Apart from these reports, little is known about the host range of the net blotch pathogen in California and the possible role certain species may have in harboring or perpetuating the inoculum of *P. t. teres*. The purpose of this study was to determine the host range of isolates of *P. t. teres* from California and the potential of wild grass species as alternative hosts for the net blotch pathogen.

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MATERIALS AND METHODS

Growth chamber study. Forty-three gramineous species (49 accessions) were evaluated for their reactions to *P. t. teres* in the growth chamber. These genotypes were selected because they either have been listed as hosts of *P. t. teres* by previous authors (21), have been used as parents in intergeneric or interspecific crosses with *H. vulgare* (6,19), or are common in barley production areas of California (4). Seeds (five to seven) of each species were planted in 50 × 35 × 9 cm metal flats containing a 1:1 mix (v/v) of fine sand:peat moss (18). The barley cultivars Kombar (CI 15694) and Prato (CI 15815) were interplanted with the test species to verify the distribution and virulence of inoculum. Plants were grown in a growth chamber at 22–24 C with a 12-hr photoperiod (65.5–139.4 W m^{-2} supplied by cool-white fluorescent bulbs).

Five isolates of *P. t. teres* from *H. vulgare* (84-56-1, 85-14-1, 86-11-3, 86-78-2, and 86-80-2) and one isolate from *H. m. leporinum* (86-63-4) were used as inocula. These isolates were obtained from collections made in or near California barley fields between 1984 and 1986 (22). The isolation, increase, and storage of single conidial isolates from original leaf specimens were as described by Steffenson and Webster (22). Inoculum was prepared by placing surface-sterilized sections (2 cm^2) of barley leaf tissue (each previously infected with one of the conidial isolates and stored dry at 22 C) onto V8 juice agar (177 ml of V8 juice, 16 g of agar, and 3 g of $CaCO_3$ per liter of H_2O) and incubating at 19–23 C for 14–17 days (22). Conidia were harvested by adding sterile distilled water (3 ml) to the plate and gently scraping the agar surface with a rubber spatula. This conidial suspension was filtered through two layers of cheesecloth and adjusted to a concentration of 2×10^4 conidia per milliliter with a hemacytometer. Inoculations were made 14–17 days after planting, when the second leaves were fully extended (growth stage [GS] 12 according to Zadoks et al [29]). The host species were inoculated with the conidial suspension (14 ml) using a DeVilbiss atomizer and were placed in a chamber (20–24 C) maintained near saturation by intermittent mistings from humidifiers for 48 hr.

The infection response of plants was assessed 3 wk after inoculation by the 0–10 rating system of Tekauz (24). This rating scale is qualitative and is based on lesion size and type (morphology and degree of chlorosis). Three of the five *P. t. teres* isolates from *H. vulgare* and the isolate from *H. m. leporinum* were used in a preliminary experiment to validate the methods of inoculation, incu-

Table 1. Infection response of gramineous species to six isolates of *Pyrenophora teres* f. *teres*

Grass species	Previously reported host	*P. t. teres* isolates from *Hordeum vulgare*					*P. t. teres* from *Hordeum murinum* subsp. *leporinum*
		84-56-1	85-14-1	86-11-3	86-78-2	86-80-2	86-63-4
Kombar barley (check)	+[a]	4–5[b]	2–3	4–5	2–3	2–3	0
Prato barley (check)	+	5–6	5–6	7–8	7–8	9–10	1
Aegilops							
cylindrica Host	−	0	0	0	0	0	0
Agropyron							
bonaepartis (Spreng.) Dur & Schinz	+	0	0	0	...[c]	0	0
ciliare (Trin.) Franch.	−	2–3	1	7	2–3	1–2	0
cristatum (L.) Gaertn.	−	0	2	2–3	2–3	0	2
repens (L.) P. Beauv.	+	4–5	0	0	1	0	0
spicatum (Pursh) Lams.-Scribn. & J.G. Sm.	+	2–3	1–2	0	3–4	3–4	0
Avena							
fatua L.	+	0	0	0	0	0	0
sativa L.	+	0	0	0	0	0	0
strigosa Schreb.	−	0	0	0	0	0	0
Brachypodium							
distachyon (L.) P. Beauv.	−	1–2	1–2	1	1–2	0	1
pinnatum (L.) P. Beauv.	+	1	1	1–2	1–2	0	1
Bromus							
auleticus Trin. ex Nees	+	1	0	0	0	0	1
erectus Huds. (Syn. *B. syriacus* Boiss)	+	0	1–2	0	1	0	2
hordeaceus L. (Syn. *B. mollis* Trin.)	−	0	0	0	0	0	0
inermis Leyss.	+	1–2	0	0	3–4	0	0
rubens L.	−	0	0	0	0	0	1–2
sterilis L.	+	0	0	0	0	0	1
unioloides Kunth (Syn. *B. catharticus* Vahl)	+	1–2	1–2	1–2	1–2	0	1–2
Cynodon							
dactylon (L.) Pers.	−	1–2	0	1	1–2	...	1–2
Deschampsia							
flexuosa (L.) Trin.	−	0	0	0	0	0	0
Elymus							
angustus Trin.	−	2–3	0	5–6	1	1	1–2
arenarius L.	−	0	0	0	0	0	0
canadensis L.	+	...	...	1–2	0	...	0
dahuricus Turcz. ex. Griseb.	+	8–9	7–8	4–5	3–4	7–8	1
subsp. *excelsus* (Turcz. ex Griseb.) Tzvelev	+	6–7	0	1–2	1–2	5–6	0
giganteus Vahl	+	2	1	1–2	1–2	1	2–3
sibiricus L.	+	8–9	3–4	3–4	6–7	1–2	1–2
Festuca							
megalura Nutt.	−	0	0	0	0	0	0
Hordelymus							
europaeus (L.) Harz	−	7–8	8–9	4–5	6–7	6–7	0
Hordeum							
bogdanii Wil.	−	6–7	0	0	0	1	0
brevisubulatum (Trin.) Link							
subsp. *violaceum* (Boiss. & Hohen.) Tzvelev	−	1–2	3–4	...	4–5	1–2	0
bulbosum L.	+	0	0	0	1–2	1–2	0
jubatum L.	+	0	0	0	0	0	2
marinum Huds.	+	1–2	0	0	0	0	0
subsp. *gussoneanum* (Parl.) Thell.	+	0	0	0	0	0	0
murinum L.							
subsp. *glaucum* (Steud.) Tzvelev	−	1–2	0	1–2	1–2	0	0
subsp. *leporinum* (Link) Arcang. (Davis accession)	+	1–2	1–2	2	1–2	0	1–2
subsp. *leporinum* (Iran accession)	+	2–3	1–2	1–2	2–3	3–4	1–2
roshevitzii Bowd.	−	1–2	1	0	1–2	1	1
stenostachys Godr.	+	...	...	0	...	1–2	0
vulgare							
subsp. *spontaneum (C. Koch) Thell.*	+	4–5	4–5	3	3–4	1–2	0
Lolium							
temulentum L.	−	0	0	0	0	0	0
Secale							
cereale L. 'Merced'	+	0	0	0	0	0	0
montanum Guss.							
subsp. *anatolicum* (Guss.) Tzvelev	−	0	0	0	0	0	0
Stipa							
pulchra Hitchc.	−	3–4	0	1–2	3–4	0	0
Triticum							
monococcum L.	+	1	0	0	0	1	1
turgidum							
subsp. *dicoccum* L. em Thell.	+	1	1	1	2	2	0
subsp. *dicoccoides* L. em Thell.	+	1	0	0	0	2	0
subsp. *durum* L. em Desf.	+	1	1	0	1	1	1

[a] As compiled by Shipton et al (21), where '+' indicates the entry was and ' - ' indicates it was not previously reported as a host of *Pyrenophora teres* f. *teres*.
[b] Infection responses were based on the 0–10 scale of Tekauz (23).
[c] Missing data.

Table 2. Disease severity and infection response of gramineous species infected with *Pyrenophora teres* f. *teres* in the field

Grass species	Identification no.[a]/ seed source[b]	Origin of seed	Previously reported host[c]	Field assessments	
				Disease severity[d]	Infection response[e]
Kombar barley (check)	CI 15694/UCD	California	+	20.00	MS-S
Prato barley (check)	CI 15815/UCD	California	+	15.00	MS-S
Tifang barley (check)	CI 4407-1/UCD	California	+	0.10	R
Aegilops					
cylindrica Host	-/UCD	...	−	0.01	R
juvenalis (Thell.) Eig	-/UCD	...	−	0.01	R
ovata L.	-/UCD	...	−	0.10	R
searsii Feldman & Kisler	-/UCD	Israel	−	0.50	MS-S
triuncialis L.	-/UCD	...	+	0.01	R
ventricosa Tausch	-/UCD	...	−	0.10	R
Agropyron					
bonaepartis (Spreng.) Dur. & Schinz	PI 227344/WRPIS	Iran	+	0.00	0
ciliare (Trin.) Franch.	PI 377532/WRPIS	Japan	−	0.10	R
cristatum (L.) Gaertn.	PI 439921/WRPIS	Former Soviet Union	−	0.10	R
elongatum (Host) P. Beauv.	PI 368851/WRPIS	Maryland	−	0.01	R
fibrosum (Schrenk) Cand.	PI 383849/WRPIS	France	−	0.05	R
intermedium (Host) P. Beauv.	PI 442639/WRPIS	Turkey	−	0.01	R
var. *trichophorum* (Link) Halac.	PI 314140/WRPIS	Former Soviet Union	−	0.01	R
repens (L.) P. Beauv.	PI 440086/WRPIS	Former Soviet Union	+	0.10	R
smithii Rydb.	PI 421274/WRPIS	Kansas	−	0.00	0
spicatum (Pursh) Lams.-Scribn. & J.G. Sm.	PI 440921/WRPIS	Idaho	+	0.10	R-MR
trachycaulum (Link) Malte ex H. Lewis	PI 442444/WRPIS	Belgium	−	0.10	R-MR
violaceum (Horn.) Lang	PI 372651/WRPIS	Alaska	−	0.10	R
Avena					
fatua L.	-/UCD	California	+	0.00	0
nuda L.	-/CRL	...	−	0.00	0
sativa L.	-/UCD	Idaho	+	0.00	0
strigosa Schreb.	-/CRL	...	−	0.00	0
Brachypodium					
distachyon (L.) P. Beauv.	PI 321403/WRPIS	Israel	−	0.10	R
phoenicoides (L.) Roem. & Schult.	PI 318959/WRPIS	Spain	−	0.10	R-MR
pinnatum (L.) P. Beauv.	PI 430277/WRPIS	Ireland	+	0.10	R-MR
sylvaticum (Huds.) P. Beauv.	PI 345965/WRPIS	Norway	−	0.10	R
Bromus					
anomalus Rupr. ex E. Fourn.	PI 232199/WRPIS	Wyoming	−	0.00	0
auleticus Trin. ex Nees	PI 162779/WRPIS	Argentina	+	0.10	R-MR
bromoideus (Lej.) Crepin (Syn. *B. arduennensis* Dum. Obs. Gram.)	PI 258394/WRPIS	Israel	−	0.01	R
diandrus Roth.	-/UCD	California	+	0.50	R
erectus Huds. (Syn. *B. syriacus* Boiss.)	PI 228400/WRPIS	Iran	+	0.01	R
hordeaceus L. (Syn. *B. mollis* Trin.)	-/UCD	California	−	0.00	0
inermis Leyss.	PI 440200/WRPIS	Former Soviet Union	+	0.00	0
subsp. *pumpellianus* (Scribn.) Wagnon	PI 371709/WRPIS	Alaska	(+)	0.01	R
marginatus Nees ex Steud.	PI 241047/WRPIS	Oregon	−	0.10	R
rigidus Roth	PI 337516/WRPIS	Argentina	−	0.00	0
rubens L.	-/UCD	California	−	0.00	0
secalnus L.	PI 258466/WRPIS	Oregon	−	0.00	0
squarrosus L.	PI 254880/WRPIS	Iraq	−	0.00	0
sterilis L.	PI 233234/WRPIS	Israel	−	0.00	0
unioloides Kunth (Syn. *B. catharticus* Vahl)	PI 442081/WRPIS	Japan	+	0.01	R
Cynodon					
dactylon (L.) Pers.	-/UCD	California	−	0.10	R
Deschampsia					
caespitosa (L.) P. Beauv.	PI 433722/WRPIS	Former Soviet Union	−	0.05	R
flexuosa (L.) Trin.	PI 283244/WRPIS	France	−	0.00	0
Elymus					
angustus Trin.	PI 440318/WRPIS	Former Soviet Union	−	0.10	R
arenarius L.	PI 372695/WRPIS	Alaska	−	0.00	0
canadensis L.	PI 236608/WRPIS	Canada	+	0.10	R
condensatus Presl	PI 442483/WRPIS	Belgium	−	0.10	R-MR
dahuricus Turcz. ex Griseb.	PI 406463/WRPIS	Former Soviet Union	+	0.10	R
subsp. *excelsus* (Turcz. ex Griseb.) Tzvelev	PI 315863/WRPIS	Czechoslovakia	+	0.10	R
giganteus Vahl	PI 314928/WRPIS	Former Soviet Union	+	0.50	R-MR
glaucus Buckley	PI 387917/WRPIS	Canada	+	0.10	R
mollis Trin. in Spreng.	PI 371727/WRPIS	Alaska	−	0.50	MR-S
sibiricus L.	PI 442485/WRPIS	Belgium	+	0.10	R-MR
virginicus L.	PI 372542/WRPIS	Canada	−	0.50	R-MR
Festuca					
arizonica Vasey	PI 469218/WRPIS	New Mexico	−	0.00	0

(*continued on next page*)

[a] PI = Plant Introduction number, CI = Cereal Investigation number, CHC = Canadian Hordeum Collection number, and '-' indicates that a number has not been assigned or is unknown.

[b] WRPIS = Western Regional Plant Introduction Station, Pullman, Washington; PGRC = Plant Gene Resources Canada, Agriculture Canada, Ottawa, Canada; CRL = USDA Cereal Rust Laboratory, St. Paul, Minnesota; UCD = University of California-Davis, Davis, California; and SGC = USDA Small Grains Collection, Beltsville, Maryland.

[c] As compiled by Shipton et al (21), where '+' indicates the entry was and '-' indicates it was not previously reported as a host of *P. t. teres*. Species reported as hosts by previous investigators for which a specific taxonomic subgroup (subspecies, variety, or group) was not found infected with *P. t. teres* are denoted by the symbol '(+)'.

[d] Percentage of leaf area infected by *P. t. teres* was based on the scale of Burleigh and Loubane (3).

[e] Infection response (size and type of lesion) was based on the scale developed by Buchannon and McDonald (2), where 0 = no visible infection, R = resistant, MR = moderately resistant, MS = moderately susceptible, and S = susceptible.

Table 2. (*continued from preceding page*)

Grass species	Identification no.[a]/ seed source[b]	Origin of seed	Previously reported host[c]	Field assessments	
				Disease severity[d]	Infection response[e]
arundinacea Schreb.	PI 442119/WRPIS	Japan	−	0.00	0
dolichophylla Presl	PI 478517/WRPIS	Peru	−	0.00	0
elatior L. (Syn. *F. pratensis* Huds.)	PI 383657/WRPIS	Turkey	+	0.00	0
idahoensis Elmer	PI 344642/WRPIS	Idaho	−	0.10	R-MR
longifolia Thuill.	PI 283323/WRPIS	Sweden	−	0.00	0
megalura Nutt. (Syn. *Vulpia megalura* (Nutt.) Rydb.)	-/UCD	California	−	0.05	R
ovina L.	PI 384863/WRPIS	Iran	−	0.00	0
rubra L.	PI 422771/WRPIS	France	−	0.00	0
tenuifolia Sibth.	PI 311045/WRPIS	Romania	−	0.00	0
thurberi Vasey	PI 232300/WRPIS	Colorado	−	0.00	0
Hordelymus					
europaeus (L.) Harz	PI 442484/WRPIS	Belgium	−	0.50	R-MR
Hordeum					
arizonicum Covas	CHC 1839/PGRC	Arizona	−	0.10	R
bogdanii Wil.	CHC 1115/PGRC	Iran	−	0.10	MS-MR
brevisubulatum (Trin.) Link	CHC 1062/PGRC	Iran	−	0.10	R
subsp. *violaceum* (Boiss. & Hohen.) Tzvelev	PI 440419/WRPIS	Iran	−	0.10	R
bulbosum L.	PI 401357/WRPIS	Iran	+	0.10	R
brachyantherum Nevski subsp. *californicum* (Covas & Stebb.) Bothm. et al	CI 9734/SGC	Ethiopia	+	2.00	R-MR
chilense Roem. & Schult.	CHC 1670/PGRC	Argentina	−	0.01	R
comosum Presl.	CHC 1364/PGRC	Argentina	−	0.00	0
euclaston Steud.	CHC 1291/PGRC	Argentina	−	0.00	0
jubatum L.	CHC 1344/PGRC	Argentina	+	0.01	R
lechleri (Steud.) Schenck	CHC 1388/PGRC	Argentina	−	0.00	0
marinum Huds.	PI 223324/WRPIS	Iran	+	0.10	R
subsp. *gussoneanum* (Parl.) Thell. (Syn. *H. geniculatum* All. and *H. hystrix* Roth)	PI 203462/WRPIS	Turkey	+	0.00	0
murinum L.					
subsp. *glaucum* (Steud.) Tzvelev	PI 317429/WRPIS	Afghanistan	(+)	0.50	R-MR
subsp. *leporinum* (Link) Arcang.	PI 401363/UCD	California	+	3.00	MS-S
subsp. *leporinum*	PI 401359/WRPIS	Iran	+	0.01	R
muticum Presl	CHC 1754/PGRC	Argentina	−	0.10	R
parodii Covas	CHC 1332/PGRC	Argentina	−	0.01	R
patagonicum (Haum.) Covas	CHC 1605/PGRC	Argentina	−	0.10	R-MR
subsp. *magellanicum* (Parodi & Nicora) Bothm. et al (Syn. *H. chilense* var. *magellanicum* Par. & Nic.)	CHC 1518/PGRC	Argentina	−	0.10	R
subsp. *santacrucense* (Parodi & Nicora) Bothm. et al (Syn. *H. santacrucense* Par. & Nic.)	CHC 1422/PGRC	Argentina	−	0.10	R
subsp. *setifolium* (Parodi & Nicora) Bothm. et al (Syn. *H. setifolium* Par. & Nic.)	CHC 1555/PGRC	Argentina	−	0.50	R
procerum Nevski	CHC 1336/PGRC	Argentina	−	0.00	0
pubiflorum Hook. F.	CHC 1540/PGRC	Chile	−	0.00	0
roshevitzii Bowd.	CI 15555/SGC	Minnesota	−	1.00	R-MR
stenostachys Godr.	CHC 1295/PGRC	South Africa	+	0.10	R
vulgare L.					
var. *deficiens* (Steud.) ined.	PI 382182/SGC	Ethiopia	+	2.00	MR-MS
subsp. *spontaneum* (C. Koch) Thell.	PI 466131/SGC	Israel	+	0.10	R
subsp. *spontaneum*	PI 282583/SGC	Israel	+	3.00	MR-MS
Lolium					
multiflorum Lam.	PI 410154/WRPIS	South Africa	+	0.10	R-MR
temulentum L.	PI 302664/WRPIS	India	−	0.00	0
Phalaris					
arundinacea L.	-/UCD	California	+	0.01	R
Secale					
cereale L. 'Merced'	PI 222545/UCD	California	+	0.01	R
montanum Guss.					
subsp. *antolicum* (Guss.) Tzvelev	PI 240285/WRPIS	Turkey	−	0.01	R
subsp. *kuprijanovii* (Grossh.) Tzvelev	PI 440654/WRPIS	Former Soviet Union	−	0.01	R
vavilovii Grossh.	PI 253957/WRPIS	Afghanistan	−	0.01	R
Stipa					
pulchra Hitchc.	-/UCD	California	−	0.50	R
Triticum					
aestivum					
subsp. *sphaerococcum* L. em Thell.	PI 115818/WRPIS	India	+	0.01	R
militinae Zhuk. & Migush.	PI 115816/CRL	Former Soviet Union	−	0.10	R
monococcum L.	PI 355529/CRL	Germany	+	0.10	R
subsp. *baeoticum* L. (Boiss.)	PI 355454/CRL	Germany	+	0.01	R
subsp. *urartu* (Thum.) Löve	-/UCD	Turkey	−	0.10	R
turgidum L.	PI 088737/CRL	Greece	+	0.01	R
subsp. *dicoccum* L. em Thell.	PI 355462/CRL	Germany	+	0.00	0
subsp. *dicoccoides* L. em Thell.	PI 355455/CRL	Germany	+	0.01	R
subsp. *dicoccoides* race pyramidale (L.) Perc.	PI 115814/CRL	Former Soviet Union	+	0.01	R
subsp. *durum* L. em Desf.	PI 355087/CRL	Iran	+	0.01	R
subsp. *polonicum* (L.) Löve	PI 134945/CRL	Portugal	−	0.00	0
subsp. *turanicum* (Jacubz.) Löve	PI 127106/CRL	Afghanistan	−	0.01	R

bation, and disease assessment. Data from this pilot experiment were very similar to those obtained in the complete and final inoculation experiment. In this paper, only data from the complete experiment are presented. The experiment was arranged in a completely randomized design with three replicates. Data in Table 1 represent the maximum disease rating on genotypes across the three replicates. Leaf tissue from host species exhibiting lesions was cultured on water agar to confirm infection by *P. t. teres.*

Field study. Ninety-five grass species (116 accessions) were evaluated for their reaction to *P. t. teres* in the field at the University of California Armstrong Plant Pathology farm near Davis. Seeds of each entry were sown into 16.5 × 12.7 cm clay pots containing the fine sand–peat moss potting mix (18) and were grown in a greenhouse at 22–27 C. After 1 mo, plants were set outside the greenhouse for 10–14 days to acclimate to ambient conditions and were then transplanted to the field on 17 December 1986. The grass species (three replicates per species) were arranged in a completely randomized design and were spaced 0.3 m apart in four 37-m rows. To augment pathogen spread in the nursery, a spreader row of the susceptible barley cultivar Prato was planted around the rows of grass species. The nursery was inoculated by placing infected barley straw (naturally infected with *P. t. teres* from the previous season) over the plants (40 g of straw per meter of row) when most were at the midtillering stage (GS 20-28). The susceptible barley cultivars Kombar and Prato and the resistant genotype Tifang (CI 4407-1) were each replicated 10 times in the plot as checks. Sprinkler irrigation was applied four times (approximately 50 mm per application) during the season to increase the development of disease in the nursery.

Infection response (size and type of lesion) and disease severity (percentage of leaf area infected with *P. t. teres*) were assessed every 2 wk on the leaves of grass species using the rating scales developed by Buchannon and McDonald (2) and Burleigh and Loubane (3), respectively. Final disease assessments (Table 2) were made on 19 May 1987, when most entries were in the heading stage (GS 51-60). Leaf samples from species exhibiting any type of foliar disease symptom were collected, surface sterilized, and cultured on V8 juice agar to induce sporulation of putative leaf spot pathogens. Conidia resembling those of species in the genus *Drechslera* were increased in pure culture and inoculated onto the cultivar Kombar to confirm pathogenicity. Reisolations were subsequently made from Kombar leaf tissue to corroborate infections by *P. t. teres.*

Taxonomy of species evaluated. Because many of the host species used in this study were not included in the reference by Farr et al (5), other taxonomic sources were consulted. Taxonomic designations for the genus *Hordeum* follow the naming conventions used by Von Bothmer et al (28), while designations for cultivated species of the genus *Triticum* follow Bowden (1). The remaining species from North America are designated according to Kartesz and Kartesz (9) and Crampton (4). Species from outside North America follow specific taxonomic references—Tutin et al (25) for Europe and Tzvelev and Fedorov (27) for the former Soviet Union. The taxonomy of many genera is in a state of flux. For this study, the generic designations have been conserved to agree with previous host range lists. A more current listing of genera in the Poaceae is given by Tzvelev (26).

RESULTS

Growth chamber study. Twenty-eight of the 43 gramineous species evaluated were infected by at least one of the five *P. t. teres* isolates from cultivated barley (Table 1). Fourteen of these infected species exhibited very low infection responses (small pinpoint lesions, types 1–2 on the Tekauz scale), while the other half exhibited at least some higher infection responses (types 3–9) to the isolates. Ten previously unreported host species of *P. t. teres* were identified: *Agropyron ciliare* (Trin.) Franch., *A. cristatum* (L.) Gaertn., *Brachypodium distachyon* (L.) P. Beauv., *Cynodon dactylon* (L.) Pers., *Elymus angustus* Trin., *Hordelymus europaeus* (L.) Harz, *Hordeum bogdanii* Wil., *H. brevisubulatum* (Trin.) Link subsp. *violaceum* (Boiss. & Hohen.) Tzvelev, *H. roshevitzii* Bowd., and *Stipa pulchra* Hitchc. Eighteen of 24 previously reported hosts were infected by at least one of the *P. t. teres* isolates from barley. Individual isolates varied considerably in the number of grass species they infected; isolates 85-14-1, 86-11-3, and 86-80-2 infected 16 species, whereas 86-78-2 infected 22 and 84-56-1 infected 23. Only eight host species were infected by all five isolates.

Eighteen species were infected by the *P. t. teres* isolate (86-63-4) from *H. m. leporinum.* The host range of this isolate was markedly different from those derived from cultivated barley, in that *Bromus rubens* L., *B. sterilis* L., and *Hordeum jubatum* L. were infected, and three species of *Agropyron* (*A. ciliare, A. repens* (L.) P. Beauv., and *A. spicatum* (Pursh) Lams.-Scribn. & J.G. Sm.), *Bromus inermis* Leyss., *Elymus canadensis* L., *Hordelymus europaeus,* six species of *Hordeum* (*H. bogdanii, H. brevisubulatum* subsp. *violaceum, H. bulbosum* L., *H. marinum, H. stenostachys* Godr., and *H. v. spontaneum*), and *Stipa pulchra* were not. Isolate 86-63-4 exhibited a low level of virulence (types 1–3) on all grass species it infected, including *H. m. leporinum* (Davis accession), the host from which this isolate was derived. The infection response of Prato to isolate 86-63-4 was low in comparison with the isolates derived from barley, and on Kombar no visible infections were observed.

Field study. Sixty-five of 95 gramineous species were infected with *P. t. teres* in the field (Table 2). Thirty-eight of these species represent new hosts, including eight *Hordeum* species. Additionally, four genera were newly identified as containing host species: *Cynodon, Deschampsia, Hordelymus,* and *Stipa.* Twenty-seven of 31 previously reported hosts of *P. t. teres* were infected in the field. Leaf tissue from all species exhibiting leaf spot symptoms produced conidia that were morphologically identical to the anamorph of *P. t. teres* in culture. Moreover, inoculum from these cultures produced typical net blotch lesions on the barley cultivar Kombar. Reisolation of *P. t. teres* from Kombar leaf tissue was successful for cultures derived from all species except *Bromus auleticus* Trin. ex Nees. Twenty-seven of 38 gramineous species commonly found in California (not specifically designated in Table 2) were infected in this study. Thirteen of these species frequently occur in or near the barley growing areas of California (4): *Aegilops triuncialis* L., *Agropyron repens, Brachypodium distachyon, Bromus diandrus* Roth, *Bromus marginatus* Nees ex Steud., *Cynodon dactylon, Elymus condensatus* Presl., *Festuca megalura* Nutt., *Hordeum jubatum, H. m. glaucum, H. m. leporinum, Lolium multiflorum* Lam., *Secale cereale* L., and *Stipa pulchra.* Of the 65 hosts identified in this experiment, most exhibited small and dark necrotic lesions, which in some cases expanded to form light brown elliptical lesions with little or no chlorosis. *H. m. leporinum* was the only wild grass species to exhibit the netted lesions typically observed on genotypes of *H. vulgare* susceptible to virulent isolates of *P. t. teres.*

DISCUSSION

A large portion of the previously reported host range for *P. t. teres* was confirmed in this study by using isolates from California. Differences in host range were observed between the California isolates and those from other areas of the world. The most notable differences were the absence of infection on species in the genus *Avena* and the few species infected in the genus *Bromus* by isolates from California (Tables 1 and 2). Such differences are not surprising given that distinct pathotypes of *P. t. teres* are known in many barley-producing regions (21,22). Indeed, even in this study, differences for host range were observed among the six isolates tested in the growth chamber. Thirty-eight new hosts of *P. t. teres* were identified in this study, considerably enlarging the host

range of the pathogen from 47 (21) to 85 host species. Thus, California isolates of *P. t. teres* exhibit a fairly broad host range.

In this study, 13 grass species that commonly occur in or near the barley-producing regions of California were infected in the field. Additionally, we demonstrated that a single passage of *P. t. teres* through any of these wild grass hosts does not significantly reduce the virulence of the pathogen on cultivated barley. The data suggest that these wild grass species may play a role in the epidemiology of net blotch in California. In Israel, there are wild grass species that can have a major impact on the epidemiology of net blotch (13). If such a species exists in California, our data suggest that it could be *H. m. leporinum.* This species is a common weed in California and was the only alternative host (besides *H. m. glaucum*) found naturally infected in the field. In 1986, the net blotch pathogen was isolated from *H. m. leporinum* plants in 27 of 122 sites surveyed in California (B. J. Steffenson, *unpublished*). Most of these sites were near commercial barley fields. In the field test, this species was the only alternative host to exhibit a disease severity greater than 1% and a moderately susceptible to susceptible lesion type (Table 2). Moreover, conidia of *P. t. teres* have been observed on *H. m. leporinum,* both on the leaf surface during the growing season and on senescent straw in the field (M. P. Brown, *unpublished*). These data suggest that *H. m. leporinum* is the wild host of greatest significance for the net blotch pathogen in California. However, a single isolate of *P. t. teres* from *H. m. leporinum* displayed evidence of specialization as indicated by the low (resistant) infection responses on the barley cultivars Prato and Kombar in the growth chamber. Similar results were reported for *P. t. teres* isolates from this host in Australia (14). Further research is needed to determine if isolates of *P. t. teres* from *H. m. leporinum* are indeed specialized to host, because our evidence is based on only one isolate.

The purpose of this study was to determine the host range of California isolates of *P. t. teres* and the potential of these hosts as sources of primary inoculum for the net blotch pathogen. We conclude that California isolates exhibit a broad host range under field conditions; however, the role of wild hosts in actually initiating net blotch epidemics is still unresolved. With the exception of *H. m. leporinum,* all wild hosts exhibited small necrotic lesions similar to those observed by Frecha (7) and Kenneth (11) in their host range studies. Keeling and Banttari (10) observed similar lesion types on resistant barley genotypes infected with *P. t. teres* and demonstrated that these infected leaves could support sporulation of the pathogen. It is possible that wild hosts exhibiting small restricted lesions could function in the spread of *P. t. teres* inoculum. However, if host-specific pathotypes exist in California, the role of these alternative hosts in the epidemiology of barley net blotch may be limited.

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