Host Ranges and Interrelations of Erysiphe graminis hordei, E. graminis tritici, and E. graminis avenae

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ABSTRACT

Each of the three varieties, *Erysiphe graminis hordei, E.graminis tritici,* and *E.graminis avenae* possess a wider host range in Israel than elsewhere. The first variety attacked accessions of 37 species representing 18 genera of the tribes Hordeae, Aveneae, Festuceae, and Stipeae. Isolates of *E. graminis tritici* attacked entries of 47 species belonging to 16 genera of the above four tribes. Accessions of 31 species of 20 genera representing the same tribes were compatible with *E.graminis avenae.* Hosts receptive to cultures of two varieties of *E. graminis* were found. They were congenial with either *E.graminis hordei* and *E.graminis tritici, E. graminis hordei* and *E.graminis avenae,* or *E.graminis tritici* and *E.graminis avenae.* Possibly, hosts harboring different varieties of *E.graminis* will facilitate their intercrossing.

Phylogenetic aspects of the results obtained are discussed. Phytopathology 60:628-634.

Israel is part of one of the centers of origin and diversification of the wild ancestors and relatives of cultivated barley, wheat (12), and oats (25). Stebbins (28) postulates that the major trends in the phylogenetic development of grasses "were accompanied by a series of cycles of divergent and convergent or reticulate evolution, the latter being brought about by hybridization and chromosome doubling, or amphiploidy". This hypothesis implies the existence of a wide heterogeneity in the indigenous populations of *Hordeum, Triticum,* and *Avena* species and intergradation of genetic characters at various levels of biologic and morphologic specialization.

The concept of correlated evolution of the constituents of the host-obligate parasite system suggests that a corresponding genetic differentiation and intergradation is present in the powdery mildew species *Erysiphe graminis* DC. attacking the local *Hordeum, Triticum,* and *Avena* flora (6). The common occurrence of the effectively functioning sexual stage of the fungus on some grasses in nature, and the well coordinated seasonal development of the parasite and some hosts (19) make this supposition even more plausible.

The present research was undertaken to obtain more information regarding the parasitic specialization of the powdery mildew fungi on barley, wheat, and oats, and the extent of their host range in this geographic region.

Early literature dealing with parasitic specialization of *Erysiphe graminis* was reviewed by Hardison (10). Marchal (see 10) distinguished seven specialized forms in *E.graminis* (referred to hereafter as "varieties"), *tritici* on *Triticum* spp., *hordei* on *Hordeum* spp., *secalis* on *Secale* spp., *avenae* on *Avena* spp. and *Arrhenatherum* spp., *poae* on *Poa* spp., *agropyri* on *Agropyron* spp., and *bromi* on *Bromus* spp. Before Hardison, the prevailing opinion was that each of these varieties was mostly restricted to a single genus. Hardison (10, 11) invalidated this concept of narrow specialization, as his cultures infected plants of two or more genera, some of which belonged to a tribe other than the source host. However, none of the cultures isolated from plants of the tribe Hordeae was compatible with plants from other tribes. Hardison's findings, relative to the infectivity of the powdery mildew organisms on plants of more than one genus or even more than one tribe (10, 11), were confirmed by other investigators. Grasso (9) succeeded in establishing infection with *E.graminis tritici* isolated from wheat on hosts of two genera of the tribe Festuceae. Similarly, Mühle & Frauenstein (23, 24) infected a number of grass species with inocula isolated from hosts representing other tribes. Hirata (15) indicated that the host range of *E.graminis* embraces closely related or intrageneric plants as well as taxonomically far-removed genera or tribes. Blumer (2) concluded that refined infection methods make Marchal's old concept of specialized forms meaningless.

In obvious contrast are Cherewick's (3) results, revealing that in hundreds of cross inoculations "with one possible exception, no variety of *E.graminis* was able to attack the hosts of other varieties".

MATERIALS AND METHODS.—Our studies were made in 1963-1964, repeated and amplified in 1964-1965 and 1966-1967. The preponderant majority of plants subjected to inoculation were wild grasses of Israel; only in the 1st year were some grasses of outside origin included. Local grasses were identified with the aid of the key by Eig et al. (7). Cultivated cereals were represented by the genera *Hordeum, Triticum, Avena,* and *Secale.* Powdery mildew cultures used for inoculation were increased on barley cultivars Manchuria, C.I. 2330 and Manchuria, C.I. 2947, both received together with the International Barley Disease Nursery (IBDN) of the USDA; wheat (our principal vulgare cultivar Florence × Aurore, known as F.A. 8193 also, and the local durum wheat Oued-Zenati × Bouteille, ordinarily referred to as Z.B.); and oats (local cultivars Fulghum and Mulga). The fungus cultures were composites of

isolates originally secured from cultivated barley, wheat, and oat crops from different parts of the country to insure thus a wide range of parasitic diversity. The parasitic heterogeneity of isolates from barley was obviated in their performance on differentials employed for race identification of *E.graminis hordei* (21). Similar parasitic variation was manifested in the performance of isolates derived from wheat on differentials of *E.graminis tritici* (27). Data of tests with isolates of *E.graminis avenae* on differentials of Hayes & Jones (14) are not sufficient for drawing conclusions as to their parasitic specialization. Ordinarily, such isolates were derived from conidia. But in 1964-1965, parallel tests were run with *E.graminis hordei* and *E.graminis tritici* of both conidial and ascosporic origin. The latter ones were obtained by resorting to the following procedure. Filter paper caps of glass chimneys protecting healthy barley or wheat seedlings were replaced by bottoms of petri dishes lined with barley or wheat straw collected the preceding summer and carrying fertile cleistothecia at the time of the inoculation test. Upon exposure for a minimum of a 72-hr period to 20 ± 2 C at high humidity, the petri dishes were substituted by filter paper covers. Generally, good infection was accomplished, and the conidia produced were studied for their host range (Table 1). We presume that the incited infection was of ascosporic origin, since the cleistothecia involved were found to be fertile, and ascospores liberated from ripe cleistothecia are germinable and infectious (19). Furthermore, we repeatedly failed in our attempts to secure viable conidia from barley and wheat straw brought from the fields in summer. In host range studies, 3 to 10 seeds of each grass collection were planted in sterilized soil in plastic containers 2.5 cm in diam and 4 cm high. Nutrient solution was added once or twice during the experiment. These containers were enclosed immediately after sowing in plastic chambers covered with cheesecloth pads 5-6 layers thick. The emerging seedlings were inoculated at least twice, first at the one-leaf stage, then 4-6 days later.

TABLE 1. Number of host collections[a] inoculated with the respective varieties of *Erysiphe graminis*, and the distribution of their genera and species

Inoculum	Year of testing	No. collections tested[b]	No. genera tested	No. species tested
E.g.hordei conidial origin	1963-64	306	42	139
E.g.tritici conidial origin		269	44	136
E.g.avenae conidial origin		301	44	145
E.g.hordei conidial origin	1964-65	368	55	126
ascospore origin		369	58	131
E.g.tritici conidial origin		362	57	122
ascospore origin		416	58	146
E.g.avenae conidial origin		358	56	129
E.g.hordei conidial origin	1966-67	136	49	98
E.g.tritici conidial origin		136	44	94
E.g.avenae conidial origin		135	45	93

[a] Each collection was produced by seed bulked from more than one plant.

[b] Some of the collections were tested more than one season.

Fungus cultures subsequently used in inoculation experiments were increased on the respective cultivars of barley, wheat, and oats under glass chimneys topped with filter paper covers. Plants on which a heavy cast of powdery mildew developed were transferred to the plastic chambers with the grass seedlings chosen for testing. Upon removing the glass chimneys, such plants were tapped over these seedlings previously atomized with water containing as a surfactant Tween-20 (polyoxyethylene sorbitan monolaurate). Then the plastic chambers were again covered with the cheesecloth pads. By inoculating inside plastic chambers placed in closed greenhouse compartments, the danger of chance contamination from airborne spores was obviously minimized. Records were taken at least twice, at 10 and at 14-16 days after inoculation. Containers, with seedlings showing successful infection, were transplanted to larger pots and maintained for 5-7 days under glass chimneys capped with filter paper before inoculation of barley, wheat, and oat cultivars in ensuing trials. This precaution was taken to eliminate conidia which might have reached the grass without causing infection. As shown by preliminary experiments, such conidia retain their viability for no more than 4 days. Conidia produced as a result of infection, were transferred with the aid of a camel's-hair brush to healthy seedlings of barley, wheat, and oat cultivars isolated under glass chimneys. Only cultures capable of infecting seedlings of the cultivar on which they have been originally increased were considered as compatible with the artificially inoculated grass host from which they were reisolated.

Cultivars of barley, wheat, and oats are narrowly specialized in their compatibility with varieties of *E.graminis*, and the possibility of their becoming infected with varieties of powdery mildew other than their own seems to be remote (Table 2, and *unpublished data*). Plainly, this factor reduces the danger of contamination in the described inoculation tests.

RESULTS.—*Incompatible grasses.*—The following grass species were not hosts to any of the powdery mildew cultures tested (because of difficulties in seed germination, a few accessions could not be tested with all three cultures): *Aegilops bicornis* (Forsk.) J.et S.; *A.biuncialis* Vis.; *A.triuncialis* L.; *Agropyrum cristatum* (L.) Gaertn.; *A.junceum* (L.) P.B.; *Agrostis alba* L.; *A.palustris* Huds.; *A.verticillata* Vill.; *Alopecurus myosuroides* Huds.; *A.ventricosus* Pers.; *Andropogon distachyus* L.; *A.hirtus* L.; *A.scoparius* Michx.; *Aristida caerulescens* Desf.; *A.lanata* Forsk.; *Arrhenatherum elatius* (L.) Presl; *Boissiera squarrosa* Banks et Sol.; *Brachypodium distachyum* (L.) Roem. & Schult.; *B. pinnatum* (L.) R. & S.; *Briza maxima* L.; *B.minor* L.; *Bromus aegyptiacus* Tausch; *B.alopecurus* Poir.; *B. carinatus* Hook. & Arn.; *B.ciliatus* L.; *B.danthoniae*

TABLE 2. Species of Gramineae with plants receptive to the indicated varieties of *Erysiphe graminis*

Host	*E.g.hordei*	*E.g.tritici*	*E.g.avenae*
Tribe Hordeae[a]			
Aegilops			
crassa Boiss.		11[b]	
cylindrica Host	0[c]	12	0
kotschyi Boiss.	13, 14	13, 16, 17	0
longissima Schw. & Muschl.	0	25	0
ovata L.	29	27-29, 32	0
peregrina (Hack.)Eig	0	47-52	0
sharonensis Eig	0	33, 34, 38	0
speltoides Tausch	0	43	0
squarrosa L.	0	39, 40	0
umbellulata Zhuk.	0	54	0
Agropyrum			
elongatum (Host) P.B.	0	60, 63	0
panormitanum Parl.	66, 67	66, 67	0
spicatum (Pursh)Scribn. & Smith	68	68	0
Elymus			
caput-medusae L.	264-269, 272	266-269, 271-273	0
condensatus Presl	0	274	0
dahuricus Turcz.		275	0
geniculatus Del.	276, 278-280	276, 278-282	276
junceus Fisch	285	284, 285	0
paboanus Claus	0	286	0
Eremopyrum			
buonapartis (Spreng.)Nevski	292-294, 297, 298	292, 296-298	292-294
Hordeum			
bulbosum L.	323, 325, 326, 328, 330, 331	326	0
depressum (Scribn. & Smith)Rydb.	332	0	0
gussonianum Parl.	333	0	0
irregulare Aberg et Wiebe	335	0	0
marinum Huds.	338-342	342-344	0
murinum L.(+ *H.leporinum* Link)	345, 347, 349-355	0	0
sativum Jess.	356	0	0
spontaneum C.Koch	357-362	0	0
stebbinsii Covas	364, 365, 367	0	0
Pholiurus			
filiformis (Roth)Schinz & Thell.	0	471	0
Psilurus			
incurvus (Gou.)Schinz & Thell.	504	505	0
Triticum			
aegilopoides Thurb.	0	558-561	0
aethiopicum Jakubz.	0	562	0
boeoticum Boiss.	0	563	0
dicoccoides Koern.	0	564-575	0
dicoccum Schrank	0	577-579	0
durum Desf.	0	581	0
monococcum L.	0	582-583	0
paleocolchicum Men.	0	589	0
vulgare Host(var.Rescue)	0	593	0
Tribe Festuceae			
Ammochloa			
palaestina Boiss.	0	0	84
Bromus			
fasciculatus Presl	159, 160	0	0
madritensis L.	182	0	0
rubens L.	192	0	0
scoparius L.	193, 197, 198	193, 197, 198	0
tectorum L.	212	214	0
Cutandia			
philistea (Boiss.)Bth.	235	231, 232	232, 235
Echinaria			
capitata (L.) Desf.	261	0	0
Lamarckia			
aurea (L.) Moench.	386	0	386-389
Lolium			
gaudini Parl.	0	0	393
subulatum Vis.	411	0	0
Poa			
sinaica Steud.	0	0	490
Sclerochloa			
dura (L.) P.B.	0	0	509
Sphenopus			
divaricatus (Gou.)Rchb.	534, 535	534, 535	534, 535

TABLE 2. (Continued)

Host	*E.g.hordei*	*E.g.tritici*	*E.g.avenae*
Vulpia			
aetnensis Tineo	0	594, 595	594
bromoides (L.) Gray	0	598	599
membranacea (L.) Lk.	600	600	601
myurus (L.) Gmel.	0	603, 604	603, 604
Tribe Aveneae			
Alopecurus			
utriculatus Banks et Sol.	79	0	0
Arrhenatherum			
palaestinum Boiss.	0	0	91, 94, 96
Avena			
barbata Pott.	0	0	99-103, 105
byzantina C.Koch	0	0	107
longiglumis Dur.	0	0	108, 109
sterilis L.	0	0	110-117
strigosa Schreb.	0	0	120
wiestii Steud.	0	122	121-123
Corynephorus			
articulatus (Desf.) P.B.	223	0	223
Gastridium			
ventricosum (Gou.) Schinz & Thell.	0	0	313
Gaudinia			
fragilis (L.) P.B.	0	0	316
Holcus			
annuus Salzm.	0	0	318
Koeleria			
phleoides (Vill.) Pers.	0	374	370, 377
Lagurus			
ovatus L.	0	0	381-383
Trisetum			
flavescens (L.) Beauv.	0	0	547
glumaceum Boiss.	548	548	548
koelerioides Bornm. & Hack.	550	549, 551	549-551
lineare (Forsk.) Boiss.	0	554	552-555
macrochaetum Boiss.	557	0	
Tribe Stipeae			
Oryzopsis			
caerulescens (Desf.) Hack.	418	0	0
holciformis (M.B.) Hack.	422	422	0
Stipa			
bromoides (L.) Doerfl.	537	0	0
tortilis Desf.	538, 541	0	0
sp.			545

[a] Classification of genera into tribes is that of Post (26) and Stebbins & Crampton (29).
[b] The listed figures indicate collection numbers with plants successfully infected.
[c] 0 = no infection.

Trin.; *B.inermis* Laeyss.; *B.japonicus* Thbg.; *B.lanceolatus* Roth.; *B.rigens* L.; *B.squarrosus* L.; *B.sterilis* L.; *B.syriacus* Boiss. & Bl.; *Calamagrostis epigeios* (L.) Roth; *C.pseudophragmites* (Hall.f.) Koeler; *Cenchrus echinatus* L.; *Chloris guayana* Kth.; *Cornucopiae involucratum* L.; *Cutandia maritima* (L.) Bth.; *C. memphitica* (Spreng.) Bth.; *Cynosurus coloratus* Lehm.; *C.echinatus* L.; *C.elegans* Desf.; *Dactylis glomerata* L.; *Dactyloctenium aegyptium* (L.) Richt.; *Digitaria sanguinalis* (L.) Scop.; *Echinochloa colonum* (L.) Lk.; *E.crus-galli* (L.) P.B.; *Eleusine indica* (L.) Gaertn.; *Elymus interruptus* Buckl.; *E.sibiricus* L.; *E.triticoides* Buckl.; *E.virginicus* L.; *E.wiegandii* Fernald; *Eragrostis megastachya* (Koel.) Lk.; *Eremopyrum orientale* (L.) J. & Sp.; *Festuca arundinacea* Schreb.; *F. elatior* L.; *F.rubra* L.; *Heleochloa schoenoides* (L.) Host; *Holcus lanatus* L.; *H.mollis* L.; *Hordeum hystrix* Roth; *H.jubatum* L.; *Koeleria cristata* (L.) Pers.; *K.setacea* DC.; *Lepturus cylindricus* (Willd.) Trin.; *Lolium multiflorum* Lam.; *L.perenne* L.; *L.rigidum* Gaud.; *L.temulentum* L.; *Oryzopsis miliacea* (L.) Asch. & Schw.; *Panicum antidotale* Retz.; *P.virgatum* L.; *Paspalum distichum* L.; *Pennisetum glaucum* (L.) R.Br.; *P.asperifolium* (Desf.) Kth.; *Phalaris arundinacea* L.; *P.brachystachys* Lk.; *P.bulbosa* L.; *P.canariensis* L.; *P.minor* Retz.; *P.paradoxa* L.; *Phleum arenarium* L.; *P.pratense* L.; *P.subulatum* (Savi) A. & G.; *Pholiurus incurvus* (L.) Schinz & Thell.; *Pilgerochloa blanchei* (Boiss.) Eig; *Poa bulbosa* L.; *P.compressa* L.; *P.exilis* (Tomm.) Murb.; *P.nemoralis* L.; *P.pratensis* L.; *P.trivialis* L.; *Polypogon maritimus* Willd.; *P.monspeliensis* (L.) Desf.; *Schismus arabicus* Nees.; *S.barbata* (L.) Thell.; *Scleropoa rigida* (L.) Griseb.; *Secale anatolicum* Boiss.; *S.cereale* L.; *S.montanum* Guss.; *Setaria verticillata* (L.) P.B.; *Sitanion hystrix* (Nutt.) J.G. Smith; *Sorghum almum* L.; *S.halepense* (L.) Pers.; *Trichachne californica* (Benth.) Chase; *Triticum timopheevi* Zhukov.; and *Vulpia brevis* Boiss. & Ky.

Host range of E.graminis hordei.—Seedlings of 60 genera of grasses (Table 2) were inoculated with *E.graminis hordei.* Representatives of the following

18 genera belonging to 4 tribes were compatible with the parasite (in the following fractions in brackets, the numerator designates the number of species successfully infected in the genus concerned; the denominator indicates the total number of species tested in that genus): *Aegilops* (2/13), *Agropyrum* (2/5), *Elymus* (3/7), *Eremopyrum* (1/2), *Hordeum* (8/10), *Psilurus* (1/1)—of the Hordeae tribe; *Alopecurus* (1/3), *Corynephorus* (1/1), *Trisetum* (3/5)—of the Aveneae tribe; *Bromus* (5/17), *Cutandia* (1/3), *Echinaria* (1/1), *Lamarckia* (1/1), *Lolium* (1/6), *Sphenopus* (1/1), *Vulpia* (1/5)—of the Festuceae tribe; *Oryzopsis* (2/3), *Stipa* (2/2)—of the Stipeae tribe.

Significantly, none of our cultures visibly induced infection on either of the tested *Avena* or *Triticum* plants.

In parallel experiments, inoculations were executed with a composite of 4 cultures of ascospore origin (Table 1). Their host range was similar to that of cultures arising from conidia collected in the fields.

Host range of E.graminis tritici.—Seedlings of 62 genera of grasses (Table 2) were tested for their reaction to wheat powdery mildew fungus. Infection was established with plants of the following 16 genera of four tribes, *Aegilops* (10/13), *Agropyrum* (3/5), *Elymus* (5/6), *Eremopyrum* (1/2), *Hordeum* (7/10), *Pholiurus* (1/2), *Psilurus* (1/1), *Triticum* (9/10)—of the Hordeae tribe; *Avena* (1/6), *Koeleria* (1/3), *Trisetum* (3/5)—of the Aveneae tribe; *Bromus* (2/17), *Cutandia* (1/3), *Sphenopus* (1/1), *Vulpia* (4/5)—of the Festuceae tribe; *Oryzopsis* (1/3)—of the Stipeae tribe.

Compatibility of the investigated powdery mildew cultures with *Avena* and *Hordeum* plants is of special interest. It is noteworthy that some of the *Hordeum* collections receptive to *E.graminis tritici* were immune to *E.graminis hordei* (collections 343, 344, Table 2).

One culture descended from ascospores was included in the above tests (Table 1). Its host range was not different from that of conidial cultures not derived from ascospores.

All *Triticum* species, except *T.timopheevi,* contained susceptible plants.

Host range of E.graminis avenae.—Seedlings of 58 genera of grasses (Table 2) were inoculated with *E.graminis avenae.* Accessions of the following 20 genera belonging to four tribes were successfully infected; *Elymus* (1/11), *Eremopyrum* (1/2)—of the Hordeae tribe; *Arrhenatherum* (1/2), *Avena* (5/6), *Corynephorus* (1/1), *Gastridium* (1/1), *Guadinia* (1/1), *Holcus* (1/3), *Koeleria* (1/3), *Lagurus* (1/1), *Trisetum* (1/4)—of the Aveneae tribe; *Ammochloa* (1/1), *Cutandia* (1/3), *Lamarckia* (1/1), *Lolium* (1/6), *Poa* (1/7), *Sclerochloa* (1/1), *Sphenopus* (1/1), *Vulpia* (4/5)—of the Festuceae tribe; *Stipa* (1/3)—of the Stipeae tribe. Practically each collection of *Avena barbata, A.byzantina, A.longissima, A.sterilis, A.strigosa,* and *A.wiestii* contained plants receptive to local isolates of *E.graminis avenae.*

The wide host range of our cultures contrasts with the restricted parasitic ability of Hardison's (11) isolates: his were confined to species of the three genera *Avena, Trisetum,* and *Arrhenatherum.* Significantly, despite their parasitic versatility, none of the local cultures obtained from oats were compatible with *Hordeum* or *Triticum* accessions tested.

Search for a common host of two or more varieties of E.graminis.—The wide host range of the investigated powdery mildew fungi and the ability of some of these fungi to reproduce sexually under local conditions (19) prompted a search for plants compatible with 2 or more varieties of *E.graminis* to facilitate intercrossing (10). According to Johnson (17), varieties of *Puccinia graminis* having a common host "are rather readily interfertile". Fertility of some of the intervarietal hybrids in *E.graminis* was demonstrated by Hiura (16).

The search for such hosts was carried out in grass collections, components of which were proven to be receptive to different varieties of *E.graminis* (Table 2). For example, all three varieties, *E.graminis hordei, E.graminis tritici,* and *E.graminis avenae* have congenial hosts in each of the following collections: 276 of *Elymus geniculatus*; 292 of *Eremopyrum buonapartis*; 534 and 535 of *Sphenopus divaricatus*; and 548 of *Trisetum glumaceum.*

Both *E.graminis hordei* and *E.graminis tritici* are infectious to different plants in the same collections of *Aegilops kotschyi, A.ovata, Agropyrum panormitanum, A.spicatum, Elymus caput-medusae, E.geniculatus, E. junceus, Eremopyrum buonapartis, Hordeum bulbosum, H.marinum, Oryzopsis holciformis, Bromus scoparius,* and *Vulpia membranacea* (Table 2).

E.graminis hordei and *E.graminis avenae* have congenial hosts in the same collections of *Corynephorus articulatus, Cutandia philistea, Eremopyrum buonapartis, Lamarckia aurea,* and *Trisetum koelerioides* (Table 2).

E.graminis tritici and *E.graminis avenae* inhabit plants of the same collections of *Avena wiestii, Cutandia philistea, Trisetum koelerioides, T.lineare, Vulpia aetnensis,* and *V.myurus* (Table 2).

A total of seven seeds of each of the above collections was sown in sterilized soil in plastic containers protected by glass chimneys capped with filter paper, at the rate of one seed/container. Cultures of *E.graminis hordei, E.graminis tritici,* and *E.graminis avenae* were maintained in separate, closed petri dishes on detached leaves of barley, wheat, and oats, respectively. These cultures were inoculated individually to different blades of three-leaf-old plants. Care was taken to place the culture concerned on leaves of various ages to eliminate the effect of age on host reaction. The first reading was taken 10 days after inoculation. Subsequently, cultures isolated from the infected leaves were used for inoculating susceptible seedlings of barley, wheat, and oat cultivars previously employed for inoculum build-up. Only those grass infections which produced conidia on cultivars on which they had originally been increased were considered reliable and taken into account. All inoculations in this experiment were performed with the aid of a camel's-hair brush. The cultures involved were part of those used in the trials reported above.

None of the inoculated grasses proved to be congenial with all three varieties of *E.graminis.* However, a num-

ber of plants served as a common host to cultures of two different varieties. For instance, the varieties *E. graminis tritici* and *E.graminis hordei* were compatible with one plant in each of the four collections 276, 278, 279, and 280 of *Elymus geniculatus,* and with one plant of *Sphenopus divaricatus,* collection 535. Likewise, cultures of wheat and oat powdery mildew established infection on each of the two plants in the single collection 535 of *Sphenopus divaricatus* tested and one plant of *Trisetum koelerioides,* collection 549. *E.graminis hordei* and *E.graminis avenae* were compatible with one plant of *Corynephorus articulatus,* collection 223, and one plant of *Trisetum glumaceum* in collection 548 (collection numbers as listed in Table 2).

Components of the same grass collection frequently displayed pronounced variability in their reaction to the fungus culture tested. Probably more hosts common to two or even three varieties of *E.graminis* could be discovered by increasing the number of grass collections and the amount of pathogenetically divergent isolates in the inoculation experiments.

DISCUSSION.—The phylogenetic aspects of parasitic specialization in *Erysiphe graminis* are particularly interesting in view of the uniqueness of this species (15). By having its host range restricted to a single family, *E.graminis* conceivably represents an advanced stage in the evolution of powdery mildew fungi.

The fact that some of the progenitors of barley, wheat, and oats have their center of origin and diversification in the Mediterranean region offers an opportunity to study powdery mildew organisms parasitic on these plants in their "true" place (30), where they are "components of nature" (31).

The hypothesis of correlated host-parasite evolution implies the existence of a wide spectrum of parasitic variability in *E.graminis* in this geographic area. Data in Table 2 corroborate this supposition. The host range of the composite cultures of the varieties *E.graminis hordei, E.graminis tritici,* and *E.graminis avenae* embraces, respectively, 18, 16, and 20 genera of approximately 60 tested genera. The pattern of host distribution shows a preference for species or genera closely related to the source host, although it also involves genera and tribes phylogenetically far apart, such as Hordeae and Stipeae (28, Fig. 2).

Grass species with plants compatible with the above varieties of *E.graminis* are divided among the Hordeae, Aveneae, Festuceae, and Stipeae tribes in the following manner (figures in brackets signify the number of tested species per tribe): 17(38), 5(9), 11(34), 4(5), for the variety *E.graminis hordei*; 33(52), 5(14), 8(26), 1(3), for wheat powdery mildew; 2(13), 17(22), 11(25), 1(3), for the variety *E.graminis avenae.*

Powdery mildew and rust fungi show duality in their parasitic behavior (1, 2, 4, 8, 13, 15, 20, and others). These organisms are narrowly specialized in their ability to parasitize cultivated crop varieties, being incompatible with some members of the preferred species on one hand, yet capable of attacking plants of different species or even of remote genera or tribes on the other.

It is suggested that this behavior of the parasites on grasses is at least partially accounted for by the major trends in the evolution of grasses. According to Stebbins (28), "Most of the common species of grasses . . . contain in varying proportions gene combinations derived from two, three, four, or more separate and sometimes widely divergent ancestors". It could be expected that, owing to their genetic interrelationships, wild grasses would be congenial hosts for parasitic fungi secured from a wide gamut of hosts. Cultivated grain crop varieties, on the contrary, are man-produced in an effort to secure distinct, well-delimited entities.

Pleophagy, as revealed in the compatibility of our powdery mildew cultures with grasses of widely separated genera and tribes, is not uncommon among obligate parasites. This biologic trait of great phylogenetic significance is considered by some researchers to be a relict from antiquity (5), while others regard it as a recent development reflecting "biogenic radiation" (20).

Since powdery mildew organisms overlap in their host range, their classification into separate varieties or formae speciales has been occasionally questioned (2, 10, 11). Similar complications are encountered in cereal rusts (13, 18, 32). Yet, the system of varietal classification has not been abandoned in these organisms (18).

The investigated isolates of *E.graminis* are clearly discernible on cultivars of *Hordeum, Triticum,* and *Avena.* For this reason, abolishing varietal classification of *E.graminis* is not recommended until more information is available on the occurrence of cross infection between the above crops in the fields. Clearly, grouping powdery mildew isolates in varieties or formae speciales does not imply strict parasitic differentiation of the organisms concerned, but rather their preferred adaptability to certain hosts (13).

Possibly, the existence of a common host for more than one variety of *E.graminis* will facilitate their hybridization. The significance of intercrossing between varieties of powdery mildew was stressed by Moseman (22). In his opinion, results provided by such crossing experiments could be used in planning special studies of taxonomic and other relationships between varieties of *E.graminis* or other *Erysiphe* species from different hosts, "and cytologic, histologic, physiologic, biochemical and genetic relationships between host and pathogen".

The potential importance of greenhouse studies on the host range of plant pathogens for epidemiology was indicated by Hardison (10, 11), while other investigators doubt the relevance of greenhouse results to the development of disease in nature (8, 32).

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