Host Specialization in the Complex Species, Tilletia fusca

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ABSTRACT

Certain *Tilletia* spp. recently combined with *T. fusca* proved through cross inoculation to be highly host specific. *Tilletia bromi-tectorum* is parasitic on *Bromus* spp., primarily in the sections Eubromus, Neobromus, and Ceratochloa; *T. guyotiana* is parasitic on *Bromus* spp. in the sections Bromium and Bromopsis. Only two *Bromus* spp. were hosts of both *T. bromi-tectorum* and *T. guyotiana*. *Tilletia fusca* is parasitic only on species of *Festuca*. None of the spore collections tested was parasitic on wheat. Taxonomic implications and relationships of these bunts are discussed and three varieties are designated: *T. fusca fusca, T. fusca guyotiana,* and *T. fusca bromi-tectorum*. New host species for the *T. fusca* complex are reported. Phytopathology 61: 225-227.

Several species of *Tilletia* are recognized as parasites of cereals and grasses in the Pacific Northwest. Notable among these are the common bunts (*Tilletia caries* and *T. foetida*) and dwarf bunt (*Tilletia controversa*) of wheat which from time to time have caused severe losses to this crop. Throughout much of the Pacific Northwest, weedy grasses with life cycles similar to that of winter wheat grow in and adjacent to wheat fields. These grasses, principally annual bromes and fescues, also are commonly infected with bunt fungi. Bunt on *Bromus tectorum* L. and closely related species is generally considered to be *T. bromi-tectorum* J. Urries; that on *B. japonicus* Thernb. and *B. brizaeformis* Fisch. & Mey., *T. guyotiana* Har.; and that on annual fescues, *T. fusca* Ell. & Ev. Because of the similarity of these species to the bunts attacking wheat, they have been studied more intensively than other *Tilletia* spp. on wild grasses.

Studies on the biology of *T. bromi-tectorum* and on spore germination of this and other *Tilletia* spp. have been reported previously (10, 13). Host range and cross-inoculation studies with *T. bromi-tectorum, T. guyotiana,* and *T. fusca* have been conducted intermittently since 1955 and are reported here.

Recently, Duran & Fischer (2) reduced *T. bromi-tectorum* and *T. guyotiana* to synonomy under *T. fusca*. Although we concur with Duran & Fischer in their taxonomic treatment of the three species, for convenience of discussion in this paper we will continue to use the binomials formerly assigned to these fungi.

MATERIALS AND METHODS.—The teliospore collections used are listed in Table 1. All except one were obtained from naturally infected grasses in the Pacific Northwest. Collection 213 was obtained from *Bromus inermis* Leyss. inoculated with Collection 148 in 1961. The grasses included 30 species of *Bromus* representing 40 seed accessions and 5 species of *Festuca* representing 13 seed accessions. Seed of most of the grasses were collected from natural stands in the Pacific Northwest; seed of others were obtained from the Plant Materials Center, Soil Conservation Service, and the Plant Introduction Station, ARS, USDA, Pullman, Washington. Winter wheat cultivars used for differentiating races of common and dwarf bunt (7, 8) also were included in several tests.

The grasses and wheat cultivars were exposed to infection either by spraying the soil surface after fall seeding with a suspension of ungerminated teliospores or by spraying seedlings in the one- to three-leaf stage with a suspension of germinating teliospores. Both inoculation methods are described in previous reports on *T. bromi-tectorum* and *T. controversa* (10, 11). The latter method was the more consistent, and produced higher incidence of infection.

Not all grass species, accessions, or wheat cultivars were exposed to infection by each bunt collection each year. Moreover, several grasses were exposed to infection in several tests before infection was obtained. The amount of infection varied from 1 to 90% depending on the host, test year, and method of inoculation.

RESULTS.—The grass species infected by the bunt collections in tests during 1955-1967 are listed in Table 2. Collections 33, 133, 156, and 186 of *T. bromi-tectorum* (from *B. rigidus* Roth, *B. tectorum, B. tectorum,* and *B. marginatus* Nees, respectively) were pathogenic on *Bromus* spp. in the sections Eubromus, Neobromus, and Ceratochloa. One species of the section Bromopsis (*B. pumpellianus* Scribn.) was also infected when inoculated with Collections 156 and 186. The spore masses of the collections of *T. bromi-tectorum* used as inoculum and the spore masses in grasses infected by these collections were in all cases essentially black as described by de Urries (1) and Meiners (10).

Bunt Collections 96, 148, 173, and 213 of *T. guyotiana* (from *B. japonicus, B. japonicus, B. brizaeformis,* and *B. inermis,* respectively) were pathogenic on *Bromus* spp. in the sections Bromium and Bromopsis, but not on species in the sections Eubromus and Neobromus. One species of the section Ceratochloa (*B. marginatus*) was infected by Collection 148 and by Collection 213 derived from Collection 148. Spore masses on hosts infected by these bunt collections were light brown, like those described for *T. guyotiana* (4, 11). They were readily distinguishable from the darker spore masses of Collections 33, 133, 156, and 186 of *T.*

TABLE 1. Collections of *Tilletia* spp. used in host range studies conducted during 1955-1967

Collection no.	Host	Location, date of collection	Identification
33	*Bromus rigidis*	Mansfield, Wash.; 1948	*T. bromi-tectorum*
96	*B. japonicus*	Preston, Idaho; 1954	*T. guyotiana*
118	*Festuca octoflora*	Grand Coulee, Wash.; 1955	*T. fusca*
133	*B. tectorum*	Kennewick, Wash.; 1955	*T. bromi-tectorum*
145	*F. reflexa*	Boise, Idaho; 1955	*T. fusca*
148	*B. japonicus*	Logan, Utah; 1955	*T. guyotiana*
156	*B. tectorum*	Palmer Junction, Ore.; 1955	*T. bromi-tectorum*
166	*F. pacifica*	Odessa, Wash.; 1956	*T. fusca*
173	*B. brizaeformis*	Farmington, Wash.; 1956	*T. guyotiana*
186	*B. marginatus*	Pond's Lodge, Idaho; 1957	*T. bromi-tectorum*
213	*B. inermis*	Pullman, Wash.; 1961	*T. guyotiana*

bromi-tectorum, and from the spore masses produced in grasses inoculated with this species.

Collections 118 and 145 of *T. fusca* were parasitic only on the host species from which they were collected; i.e., *Festuca octoflora* Walt. and *F. reflexa* Buckl., respectively. Collection 166 from *F. pacifica* Piper produced bunt on this grass species and on *F. reflexa,* but not on *F. octoflora.* The spore masses of *T. fusca* were black and indistinguishable from those of *T. bromi-tectorum.* None of the bunt collections from *Bromus* spp. was parasitic on grasses of the genus *Festuca.* Likewise, none of the bunt collections of *T. fusca* from *Festuca* spp. was pathogenic on *Bromus* spp.

TABLE 2. Hosts of *Tilletia bromi-tectorum, T. guyotiana,* and *T. fusca* as determined by inoculations during 1955-1967

T. bromi-tectorum	*T. guyotiana*	*T. fusca*
Bromus spp.		*Festuca* spp.
Section Eubromus	Section Bromium	
B. madritensis L.	*B. arvensis* L.	*F. octoflora* Walt.
B. rigidus Roth	*B. brevis* Steud.	*F. pacifica* Piper
B. rubens L.	*B. brizaeformis* Fisch. & Mey.	*F. reflexa* Buckl.
B. tectorum L.	*B. commutatus* Schrad.	
Section Neobromus	*B. danthoniae* Trin.	
B. trinii Desv.	*B. japonicus* Thernb.	
Section Ceratochloa	*B. mollis* L.	
B. willdenovii Kunth	*B. popovii* Drob.	
B. marginatus Nees	*B. racemosus* L.	
B. polyanthus Scribn.	*B. scoparius* L.	
Section Bromopsis	*B. squarrosus* L.	
B. pumpellianus Scribn.	*B. valdivianus* Phil.	
	Section Bromopsis	
	B. ciliatus L.	
	B. erectus Huds.	
	B. inermis Leyss.	
	B. pumpellianus Scribn.	
	B. tomentellus Boiss.	
	Section Ceratochloa	
	B. marginatus Nees	

None of the wheat cultivars inoculated with *T. bromi-tectorum, T. guyotiana,* or *T. fusca* developed symptoms of bunt. Grass species separately inoculated with each of the three species, but on which no symptoms developed, were *B. carinatus* Hook. & Arn., *B. haenkeanus* Kunth, *B. intermedius* Gass., *B. secalinus* L., *F. megalura* Mott., and *F. myuros* L.

DISCUSSION.—From both pathological and taxonomic standpoints, the relationships of *Tilletia* spp. on cereals and grasses in the Pacific Northwest present a difficult problem. The morphological characteristics of teliospores, normally used to differentiate species of *Tilletia,* form an intergrading series in the bunts from wheat, bromegrasses, and fescues. For this reason, it is sometimes difficult to assign a particular collection of bunt to a specific species. For example, when the bunt from *B. tectorum* was first collected in the Pacific Northwest, it was identified as *T. caries* rather than as a species of the *T. fusca* complex, since it appeared to resemble the former more closely than the latter species (3).

A close relationship between the bunts on bromes and fescues and those on wheat is suggested also by their requirements for spore germination. Spores of *T. bromi-tectorum, T. guyotiana,* and *T. fusca* require low temp and light for germination as do those of *T. controversa*; but the rate of germination is intermediate between that of *T. controversa* and *T. caries* (13). A close relationship is indicated also by the intercompatibility of these species on the basis of matings of primary sporidia (12). In addition, bunts of the *T. fusca* complex occur for the most part on hosts that behave as winter annuals and whose life histories closely resemble that of winter wheat. Moreover, the common and dwarf bunt organisms share hosts with *T. bromi-tectorum* and *T. guyotiana*: both *T. caries* and *T. controversa* are parasitic on *B. erectus* Huds., *B. marginatus,* and *B. tomentellus* Boiss.; *T. controversa* is pathogenic also on *B. ciliatus* L. (6, 9).

Negative results from repeated inoculations of wheat cultivars with bunts of the *T. fusca* complex indicate that they do not contribute to the wheat bunt problem. This, plus differences in requirements for spore germination and generally consistent differences in spore morphology, indicate that the bunts of the *T. fusca* complex should continue to be considered as distinct from *T. caries* and *T. controversa* (10).

Concerning the *T. fusca* complex itself, *T. bromi-tectorum, T. guyotiana,* and *T. fusca* are difficult to distinguish on the basis of spore morphology. In characteristics such as exospore ornamentation and spore size, they tend to form an intergrading series (2, 10). Some differences in germination requirements among the three species have been noted. Individual

collections within each species, however, show considerable variation in time required for germination as well as in capacity to germinate at various temp (13).

The color of the spore mass appeared to be a reliable characteristic to differentiate *T. guyotiana* from *T. bromi-tectorum* and *T. fusca*. In all hosts, the spore masses of *T. guyotiana* were distinctly lighter in color than those of either *T. bromi-tectorum* or *T. fusca*. On the other hand, color of the spore mass could not be used to distinguish *T. bromi-tectorum* from *T. fusca*.

Results of cross-inoculation studies indicate that *T. bromi-tectorum, T. guyotiana,* and *T. fusca* can be distinguished to a large extent on the basis of host specificity. Both *T. bromi-tectorum* and *T. guyotiana* are parasitic on species of *Bromus,* but little overlapping of hosts within this genus occurs. *Tilletia bromi-tectorum* is parasitic primarily on species in the sections Eubromus, Neobromus, and Ceratochloa; *T. guyotiana* is parasitic primarily on species in the sections Bromium and Bromopsis. Only two species, *B. pumpellianus* (section Bromopsis) and *B. marginatus* (section Ceratochloa), were parasitized by both *T. bromi-tectorum* and *T. guyotiana. Tilletia fusca,* on the other hand, is parasitic only on species of *Festuca.*

The species concept for the smut fungi proposed by Fischer & Shaw (5) considers host specialization at the family level as a basis for separation of morphologically similar species. This concept seems to have received considerable acceptance, and it has provided some degree of stability in the taxonomy of an important group of plant pathogens. Thus, in view of the morphologic similarity of *T. bromi-tectorum, T. guyotiana,* and *T. fusca,* we concur with Duran & Fischer (2) that they should be regarded as a single complex species, e.g., *T. fusca.* Having demonstrated a considerable degree of host specificity and some slight morphologic differences within this group, however, we propose to recognize within the species specialized varieties designated by trinomials. Thus, those spore collections of *T. fusca* with black spore masses and parasitic on *Bromus* spp. in the sections Eubromus, Neobromus, and Ceratochloa are designated as *T. fusca* var. *bromi-tectorum* (J. Urries) *var. nov.* Those with light brown spore masses and parasitic on *Bromus* spp. in sections Bromium and Bromopsis are designated *T. fusca* var. *guyotiana* (Har.) *var. nov.* Those with black spore masses and parasitic on annual fescues are designated *T. fusca* var. *fusca.* The use of trinomials to designate host-specialized varieties within morphologic species is well established in the cereal rusts, and has been used to some extent in other smut fungi (5). We believe the trinomial system is useful and that its use is appropriate for bunts of the *T. fusca* complex.

The following grasses reported here as hosts of *T. fusca* have not been thus reported before: *B. arvensis* L., *B. brevis* Steud., *B. willdenovii* Kunth, *B. ciliatus, B. danthoniae* Trin., *B. inermis, B. madritensis* L., *B. polyanthus* Scribn., *B. popovii* Drob., *B. pumpellianus, B. scoparius* L., *B. tomentellus, B. trinii* Desv., and *B. valdivianus* Phil. New host records for North America are *B. erectus* and *B. squarrosus* L.

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