Comparison of Host Ranges of *Tilletia indica* and *T. barclayana*

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ABSTRACT

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Fifty-eight plant species representing 21 genera within 10 tribes of the Gramineae were tested for susceptibility to *Tilletia indica* isolates from India and/or Mexico. Most of the species susceptible to *T. indica* were inoculated with isolates of *T. barclayana*, of which *Aegilops sharonensis* was the only nonrice species susceptible to *T. barclayana* and *T. indica*. Several genera were susceptible to *T. indica*: *Aegilops* (11 of 16 species), *Bromus* (two of four species), *Lolium* (three of seven species), *Oryzopsis* (one of one species), and *Triticum* (three of five species). Different accessions of the same species were not all susceptible; in some instances, different cultures of the same pathogen varied in pathogenicity on a given plant accession.

Karnal bunt of wheat, caused by *Tilletia indica* Mitra (*Neovossia indica* (Mitra) Mundkur), was first discovered in India in 1930 by Mitra (15) and has since been reported in Pakistan (17), Iraq (4), and Mexico (5). It has been found in India on wheat seed intercepted from Afghanistan (12), Lebanon, Syria, Turkey, and Sweden (10). Wheat movement into countries without Karnal bunt is regulated on an international scale and is subject to quarantine (1,2,10). This disease does not occur naturally in wheat fields in the United States, and there are no U.S. wheat (*Triticum aestivum* L. em. Thell) cultivars among those tested that are immune to infection by *T. indica*. Therefore, the detection of Karnal bunt in wheat intercepted from Mexico (2) by the Plant Protection and Quarantine division of the Animal and Plant Health Inspection Service (APHIS) of the United States Department of Agriculture (USDA) has spurred the participation of the United States in the evaluation of material grown in cooperative Karnal bunt screening nurseries in countries where this disease occurs.

The potential for Karnal bunt entry into California is of special concern to the California Department of Food and Agriculture (CDFA). Occasionally, *T. indica* teliospores are found in railroad boxcars entering California from Mexico (13). *T. indica* is difficult to distinguish from *T. barclayana* (Bref.) Sacc. & Syd., a morphologically similar smut species (14), when few teliospores are recovered or teliospores are deteriorated because of the natural variability in teliospore dimensions and exospore patterns (14,18).

Kernel smut of rice, caused by *T. barclayana*, was first discovered in Japan in 1896 by Takahashi (22) and has since been reported in most major rice production areas of the world (29). The disease cost Texas rice producers approximately $15 million in 1968 (28) and $1.2 million in 1980 (N. G. Whitney, *personal communication*).

Wheat-rice rotations are common in areas of the world where Karnal bunt of wheat and kernel smut of rice are found. There are no reports of *T. indica* infecting rice or of *T. barclayana* infecting wheat, although opportunities might exist for the two species to form interspecific hybrids on a common host. This would further complicate efforts to monitor movement of these pathogens as distinct species. If common grass hosts are susceptible to *T. indica* under natural conditions, then quarantine laws may have to be reinterpreted.

This study was undertaken to identify plant species susceptible to 1) *T. indica* and 2) also to *T. barclayana*. All experiments were performed in the containment laboratory and greenhouse facilities of the USDA Foreign Disease-Weed Science Research Unit at Fort Detrick, Frederick, MD.

MATERIALS AND METHODS

Pathogen origin. Wheat seed infected with *T. indica* was from the Yaqui and Mayo valleys, Sonora, Mexico, during 1981–1984 and was obtained from J. M. Prescott, International Maize and Wheat Improvement Center (CIMMYT), and USDA-APHIS. Wheat seed from Amritsar and Patiala, India, infected with *T. indica* was collected in 1983 and was obtained from L. M. Joshi, Indian Agricultural Research Institute (IARI), New Delhi. Rice kernels infected with *T. barclayana* were collected in 1984 in California and Texas and were obtained from T. T. Matsumoto, CDFA, and N. G. Whitney, Texas A&M University, respectively.

Plant preparation. Wheat and rice cultivars susceptible to *T. indica* and *T. barclayana*, respectively, were planted at three seeds per 12-cm-diameter clay pot containing a soil mix of silty-clay loam, sand, perlite, and peat (2:1:1:1) amended with 6.4 g of 10:10:10 fertilizer per liter and 25.7 g of lime per liter. Wheat cultivars known to be susceptible to *T. indica* and planted for use as controls were Anza, Max, Mexicali, Olaf, Yecora Rojo, Sinton, Sonalika, and Yolo. Rice cultivars known to be susceptible to *T. barclayana* and planted for use as controls were L201 and S201. These two rice cultivars were provided by T. T. Matsumoto, CDFA, and were being used commercially at the time of our study. The plants were grown in a glasshouse at 15–21 C until most of the tillers in a pot had reached the heading stage (growth stage 10–10.5.1 for wheat [11] and 4–5.9 for rice [3]).

Seed of grass species to be tested was planted in the same manner as above, unless the species had to be vernalized for flowering to occur. All *Aegilops* accessions were vernalized. Glumes were removed from the seed, and the seed was then surface-sterlized in 0.5% sodium hypochlorite for 4 min, rinsed twice in distilled water, surface-treated with a slurry of 0.1 g captan (Captan 50W) per liter of water, and dried at room temperature. Sterile screw-cap 15-ml polystyrene test tubes were filled to one-tenth of their height with vermiculite and covered with conical filter paper disks cut to approximately 1 cm^2 diameter. Distilled water was added until the vermiculite was saturated without allowing the water to collect at the bottom of the tubes. Two seeds were placed into each tube, and the tube was capped loosely to allow for gas exchange. Tubes were incubated at 2 ± 1 C with a 12-hr photoperiod at 190 $\mu E \cdot m^{-2} \cdot sec^{-1}$ for 50–60 days. Germinated seeds were removed from the tubes and

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planted as specified for pot plantings of wheat and rice.

Inoculum preparation. Both *T. indica* and *T. barclayana* cultures were maintained on potato-dextrose agar as mass transfers of mycelia from germinating teliospores or as monosporidial lines. Monosporidial lines were established on potato-dextrose agar (made from fresh potatoes) by culturing single primary sporidia isolated from germinated teliospores. All cultures were transferred every 2 wk to maintain actively sporulating cultures (19). Blocks of mycelia-containing agar were transferred to lids of petri plates, and the lids were inverted over 2% water agar and incubated at 19 ± 2 C. Sporidia that were released onto the surface of the agar after 2 wk were harvested by flooding the plates with distilled water and dislodging sporidia with a rubber policeman. Inocula from cultures started from germinating teliospores were adjusted to 10^4–10^5 sporidia per milliliter after determination of sporidial concentrations with a hemacytometer. Inocula from monosporidial-line cultures were adjusted to approximately equal concentrations before mixing compatible monosporidial lines, in pairs, for use as inocula. All species that were initially tested with compatible pairs of monosporidial lines were tested again with cultures originating from germinating teliospores. The latter may have possessed more than two mating types and potentially greater variation in virulence, since many teliospores from a natural population were used to establish the cultures.

Table 1. Proportion of plant species[a] inoculated with *Tilletia indica* or *Tilletia barclayana* showing symptoms of infection

Tribe Species	*T. indica*		*T. barclayana*	
	Accessions infected	Plants infected	Accessions infected	Plants infected
Agrostideae				
Oryzopsis miliacea (L.) Benth. & Hook. ex Aschers. & Schweinf.	1/1[b]	1/8	0/1	0/33
Andropogoneae				
Rottboellia cochinchinensis L.f.	...[c]	...	0/1	0/5
Sorghum halepense (L.) Pers.	0/1	0/12	0/2	0/26
Aveneae				
Avena barbata L.	0/1	0/6	...	...
A. fatua L.	0/2	0/18	0/1	0/17
A. sativa L.	0/3	0/93	0/1	0/27
Chlorideae				
Eleusine indica (L.) Gaertn.	0/1	0/33	...	...
Festuceae				
Bromus ciliatus L.	1/1	3/20	0/1	0/31
B. secalinus L.	0/1	0/25	...	...
B. tectorum L.	1/1	4/4	0/1	0/31
B. unioloides H.B.K.	0/1	0/17	...	...
Lolium canariense Steudel	1/1	6/43	0/1	0/33
L. multiflorum Lam.	4/12	9/46	0/3	0/43
L. perenne L.	1/3	1/13	0/1	0/12
L. persicum Boiss. & Hohen. ex Boiss.	0/1	0/5	...	...
L. rigidum Gaudin	0/1	0/2	...	...
L. subulatum Visiani	0/1	0/6	...	...
L. temulentum L.	0/1	0/4	...	...
Oryzeae				
Oryza sativa L.	0/5	0.137	>80%	>80%
Paniceae				
Cenchrus ciliaris L.	0/1	0/12	0/1	0/8
Echinochloa crusgalli (L.) Beauv.	0/1	0/21	...	...
Panicum coloratum L.	0/1	0/11	...	...
P. miliaceum L.	0/1	0/24	...	...
Pennisetum clandestinum Hochst. ex Chiov.	...	...	0/1	0/7
Setaria glauca (L.) Beauv.	...	...	0/1	0/21
S. viridis (L.) Beauv.	...	...	0/1	0/17
Phalarideae				
Phalaris angusta Nees ex Trin.	0/1	0/55	...	...
P. brachystachys Link	0/1	0/3	...	...
Taniceae				
Paspalum dilatatum Poir.	0/1	0/3	...	...
Triticeae				
Aegilops bicornis (Forsk.) Jaub. & Spach	2/2	8/15	0/1	0/22
A. caudata L.	1/1	23/55	0/1	0/32
A. columnaris Zhuk.	1/1	24/24	0/1	0/91
A. comosa Sibth. & Sm.	1/1	12/15	0/1	0/109
A. crassa Boiss.	0/1	0/30	...	...
A. cylindrica Host	1/1	1/33	0/1	0/35
A. mutica Boiss.	1/1	1/3	...	...
A. ovata L.	0/1	0/6	0/1	0/5
A. searsii Feld.	1/1	2/11	...	...
A. sharonensis Eig.	3/3	24/32	1/3	3/22
A. speltoides Tausch	0/2	0/17	0/2	0/111
A. squarrosa L.	1/1	8/14	0/1	0/12
A. triaristata Willd.	1/1	1/13	0/1	0/15
A. triuncialis L.	2/2	15/17	0/2	0/107
A. variabilis Eig.	0/1	0/13	...	...
A. ventricosa Tausch	0/1	0/28	0/1	0/17
Elymus tsukushiensis Honda	0/1	0/132	...	...
Heteranthelium piliferum Hocast. ex Jaub. & Spach	0/1	0/58	...	...
Hordeum compressum Griseb.	0/1	0/3	...	...
H. vulgare L.	0/8	0/155	0/1	0/30
Secale cereale L.	0/6	0/39	0/1	0/10
Thinopyrum intermedium (Host) Barkworth & D. R. Dewey	0/1	0/6	...	...
T. spicatum (K. Presl) D. R. Dewey	0/1	0/11	...	...
Triticale (*X. Triticosecale* Wittmack)	1/1	2/10	...	...
Triticum aestivum L. em Thell.	27/27	>80%	0/4	0/519
T. monococcum var. *boeoticum* Boiss.	1/1	1/4	0/1	0/43
T. timopheevi (Zhuk.) var. *araraticum* Jakubz.	1/1	6/8	...	...
T. turgidum var. *durum* Desf.	0/2	0/54	...	...
T. urartu Tum.	0/1	0/12	0/1	0/13

[a] Taxonomic nomenclature from Hitchcock (8), Terrell et al (24), and Waines et al (26).
[b] Numerator is number infected, denominator is number inoculated.
[c] Not inoculated.

Inoculation. All tests included wheat or rice cultivars susceptible to *T. indica* or *T. barclayana*, respectively, as controls to verify inocula pathogenicity. The growth stage and an estimate of the percentage of the flowering parts that had emerged from the boot sheaths were recorded at the time of inoculation. Plants were inoculated with an aqueous suspension of sporidia by injection into the boot (19) or by atomization of flower parts that emerged from the boot. Inoculated plants were placed into a misting tent at 15–21 C for 2–3 days to provide constant free moisture. The plants were then removed to glasshouse benches and maintained at 15–21 C for 3–5 wk until they had reached maturity. Most of the species found susceptible to *T. indica* were inoculated with isolates of *T. barclayana*. Several species that were not susceptible to *T. indica* were not inoculated with *T. barclayana*. In one experiment, monosporidial lines of *T. indica* were mixed singly with sporidia of *T. barclayana* before inoculation of wheat.

In another experiment, wheat and rice were inoculated with sporidia obtained from teliospores resulting from inoculations of a common host to *T. indica* and *T. barclayana*, respectively.

Evaluation. All inoculated plants were threshed by hand. Very small seeds were examined with a dissecting microscope for external signs of bunt. Species that formed many seeds were examined by crushing the seeds with a mortar and pestle to release any teliospores that may have been enclosed within intact bunt sori. The crushed seeds then were examined for teliospores on white filter paper with the aid of a dissecting microscope.

RESULTS

The injection of sporidia of *T. indica* or *T. barclayana* into the boot of certain accessions resulted in no seed being formed. This phenomenon occurred after several boot-inoculation attempts. After three attempts, we terminated any further boot inoculations of these accessions.

The results of inoculations with pairs of compatible monosporidial lines were the same as those with cultures originating from germinating teliospores.

T. indica. Several species were susceptible in three of 10 tribes inoculated with *T. indica* (Table 1). The taxonomic nomenclature (23,24,26) was consulted before Table 1 was constructed. The number of susceptible species (numerator) in each tribe, the number of inoculated species (denominator), and the name of the susceptible species are presented. In addition, seven lines of Chinese spring wheat that had disomic additions of the chromosome of an inbred Imperial rye in their genome were all susceptible. Most of the species that were infected by *T. indica* were inoculated by injection of sporidia into the boot. *Aegilops columnaris, A. squarrosa, A. triuncialis, Lolium canariense, L. multiflorum, L. perenne*, and *Oryzopsis miliacea* were also infected by atomizing sporidia onto exposed flower parts. Rice did not become bunted after inoculation with *T. indica* (Table 2). Attempts to produce bunt on wheat with *T. indica* recovered from *A. sharonensis* were successful. The latter teliospores from *A. sharonensis* were verified to be *T. indica* by microscopic examination.

T. barclayana. *A. sharonensis* was the only species susceptible to both *T. barclayana* and *T. indica* (Table 1). *A. sharonensis* was infected by both the boot-injection and the atomization method of inoculation. Attempts to produce bunt on rice with *T. barclayana* recovered from *A. sharonensis* were unsuccessful. The latter teliospores from *A. sharonensis* were verified to be *T. barclayana* by microscopic examination. *T. barclayana* produced identical symptoms as *T. indica* on *A. sharonensis*. *T. barclayana* did not cause bunt on wheat (Table 2) or on *Pennisetum clandestinum* Hochst. ex Chiov.

The results from inoculations of individual accessions were forwarded to the curator of the USDA National Small Grains Collection, Beltsville, MD, for permanent entry into their records. The volume of data does not permit us to present results from each individual accession in this publication.

DISCUSSION

Rice was not susceptible to infection by *T. indica* and wheat was not susceptible to infection by *T. barclayana*. Therefore, when only a few viable teliospores of an unidentified fungus are found, inoculation of rice and wheat as differential hosts may be useful to confirm an identification using morphological characters. The use of more isolates of *T. indica* and *T. barclayana* would strengthen any results that indicate nonsusceptibility.

The morphological and developmental similarities between *T. indica* and *T. barclayana* may be evidence of a potential evolutionary link, especially because both species can infect *A. sharonensis*. We were successful in producing bunt of wheat with *T. indica* recovered from *A. sharonensis*, but we could not repeat this with *T. barclayana* recovered from *A. sharonensis*. Interspecific hybridization and inheritance of characteristics between certain *Tilletia* species is common and has been investigated in detail (9). Our attempts to cross *T. indica* and *T. barclayana* on wheat by mixing single monosporidial lines of *T. indica* (that were nonpathogenic when inoculated singly onto wheat) with *T. barclayana* sporidia from genetically diverse populations of teliospores were unsuccessful. Future studies of interspecific hybridization between these two species should include *A. sharonensis* as a common host.

Tullis and Johnson (25) were able to infect two *Pennisetum* species with the kernel smut of rice pathogen, then referred to as *Tilletia horrida* Tak., but could not infect rice with a morphologically similar pathogen isolated from *Pennisetum*, referred to as *Neovossia barclayana* Bref. They proposed, however, that these two smut species were synonymous based on developmental and morphological features. The fungus causing smut of both plant species is now referred to as *T. barclayana* (Bref.) Sacc. & Syd., or *Neovossia horrida* (Tak.) Padwick & Kahn (21). The confirmation of Tullis and Johnson's work, but with floret rather than seedling inoculations, would help to clarify the taxonomic confusion regarding this pathogen. We have not been successful in producing infection of *P. clandestinum* with *T. barclayana* and therefore have not been able to repeat Tullis and Johnson's work.

Several grass species (*A. columnaris, A. squarrosa, A. triuncialis, L. canariense, L. multiflorum, L. perenne*, and *O. miliacea*) were infected by atomizing *T. indica* sporidia onto exposed flower parts that had emerged from the boot sheath at inoculation and may have significance in the potential for natural infection. The *Aegilops* species were generally more susceptible to *T. indica*, as defined by more infected kernels and more kernels with the majority of the endosperm converted into bunt sori, than the other susceptible species. Even though several *Lolium* and *Bromus* accessions had kernels that were completely bunted, the majority of kernels in a spike were symptomless. Gill and Aujla (6) found no bunted kernels to only a few bunted kernels in rye accessions that were inoculated with *T. indica*. On the basis of these observations, the wild *Aegilops* and volunteer rye may provide the best opportunity for Karnal bunt to reside on natural hosts in the United States. *A. cylindrica* and *A. triuncialis* are troublesome weeds in wheat-growing areas of the United States (8,20).

Other grasses susceptible to *T. indica* are weed species in the United States. For example, *L. multiflorum* is a major weed in California (7), *L. perenne* is ubiquitous (8,23), and *B. ciliatus* and *B. tectorum* are problem weeds in western states (8,16,23). It is possible that other grass species or accessions that were not tested may also become hosts for Karnal bunt.

At least two wheat breeding institutions—CIMMYT in Mexico and the Punjab Agricultural University in India—are now screening wheat and wheat relatives for resistance to *T. indica* (6,27). Several wheat relatives were reported to be susceptible to *T. indica* in varying degrees, and a summary of this research as of September 1987 and the results reported herein is presented in Table 3.

The results thus far include cultures of

Table 2. Results from inoculation of rice with *Tilletia indica* and wheat with *Tilletia barclayana*

Cultivar	Culture[a]	Bunted plants/ inoculated plants
Rice		
California Belle	71 × 69	0/29
Dawn	MX81-374	0/36
M9	MX81-374	0/43
Nova 66	MX81-374	0/13
S201	MX81-374	0/16
Wheat		
Anza	TBL201	0/19
Olaf	TBS201	0/102
Olaf	TBB83N1	0/108
Olaf	TBL201	0/57
Olaf	TBS201 × 41	0/96
Olaf	TBS201 × 72	0/95
Yecora Rojo	TBL201	0/19
Yolo	TBL201	0/23

[a] 71 × 69 = Mixed inoculation between compatible monosporidial lines 41 and 72 of *T. indica*, isolated from teliospores collected in India and Mexico, respectively. MX81-374 = sporidial inoculum obtained from mass transfers of mixtures of germinating teliospores from *T. indica* collected in Mexico in 1981. TBL201, TBS201, TBB83N1 = sporidial inoculum obtained from mass transfers of mixtures of germinating teliospores from *T. barclayana* recovered from rice cultivars L201, S201, and B83N1, respectively, in California in 1984. TBS201 × 41 = mixed inoculation between TBS201 and monosporidial line 41 of *T. indica*. TBS201 × 72 = mixed inoculation between TBS201 and monosporidial line 72 of *T. indica*. Lines 41 and 72 of *T. indica* are of compatible (different) mating type.

Table 3. Summary of results of inoculations of wheat relatives with *Tilletia indica* at three institutions as of September 1987

Wheat relative	Institution[a]		
	FDWSRU	CIMMYT	PAU
Aegilops bicornis (Forsk.) Jaub. & Spach	+	+	+
A. biuncialis Vis.	NR	+	NR
A. caudata L.	+	+	NR
A. columnaris Zhuk.	+	0	+
A. comosa Sibth. & Sm.	+	+	NR
A. crassa Boiss.	0	0	+
A. cylindrica Host	+	+	+
A. juvenalis (Thell.) Eig.	NR	+	+
A. kotschyi Boiss.	NR	+	+
A. longissima Schweinf. & Muschli	NR	+	+
A. mutica Boiss.	+	NR	NR
A. ovata L.	0	0	+
A. searsii Feld.	+	NR	NR
A. sharonensis Eig.	+	+	+
A. speltoides Tausch	0	0	+
A. squarrosa L.	+	+	+
A. triaristata Willd.	+	+	+
A. triuncialis L.	+	+	+
A. umbellulata Zhuk.	NR	+	NR
A. uniaristata Vis.	NR	+	NR
A. variabilis Eig.	0	+	NR
A. vavilovi (Zhuk.) Chenn.	NR	+	NR
A. ventricosa Tausch	0	+	+
Triticum monococcum var. *boeoticum* Boiss.	+	NR	+
T. timopheevi (Zhuk.) var. *araraticum* Jakubz.	+	NR	+
T. turgidum L. subsp. *dicoccoides* Korn.	NR	NR	+
T. urartu Tum.	0	NR	0

[a]FDWSRU = USDA-ARS, Foreign Disease-Weed Science Research Unit (present study); CIMMYT = International Maize and Wheat Improvement Center, Mexico (Warham et al [27]); PAU = Punjab Agricultural University, India (Gill and Aujla [6]). + = Susceptible, 0 = not susceptible, NR = not reported.

T. indica that differed at each institution, as well as plant accessions that were different or identical. It is apparent that different conclusions may be reached regarding a species susceptibility if only a few accessions of one species are tested. Gill and Aujla (6) suggested that different conclusions may be made if only a few cultures of *T. indica* are used as inoculum. The results in Table 3 emphasize that parallel screening activities can be mutually beneficial.

Our results may be useful to regulatory agencies. For example, if the grass hosts of *T. indica* are susceptible under natural conditions, then countries without Karnal bunt should be aware of the potential for entry of *T. indica* on these grasses and weed species from countries with Karnal bunt. Field studies that address this issue of natural infection may help determine whether wild or cultivated grasses would provide a means for pathogen movement. Additionally, these results may be useful to institutions that are involved in screening wheat relatives for Karnal bunt resistance.

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LITERATURE CITED

1. Anonymous. 1979. Data sheets on quarantined organisms. EPPO List A1: *Tilletia indica* Mitra. 5 pp.
2. Anonymous. 1983. U.S. quarantine of Mexican wheat: Dilemma for researchers and exporters. Diversity 5:13-14.
3. Chiarappa, L., ed. 1971. Crop Loss Assessment Methods. FAO Manual on the Evaluation and Prevention of Losses by Pests, Disease, and Weeds. Suppl. 1. Commonwealth Agricultural Bureau, Farnham, England.
4. Commonwealth Mycological Institute. 1974. Distribution Maps of Plant Diseases, No. 173. 3rd ed. Commonwealth Agricultureal Bureaux, Kew, England.
5. Duran, R. 1972. Further aspects of teliospore germination in North American smut fungi II. Can. J. Bot. 50:2569-2573.
6. Gill, K. S., and Aujla, S. S. 1986. Research on breeding for Karnal bunt resistance in wheat. Punjab Agricultural University, Ludhiana, India. 43 pp.
7. Hill, J. E. 1979. Weed control in winter cereals. Pages 68-77 in: Proc. Annu. Calif. Weed Conf. 31st.
8. Hitchcock, A. S. 1951. Manual of the Grasses of the United States. 2nd ed. U.S. Dep. Agric. Misc. Publ. 200. 1,051 pp.
9. Holton, C. S. 1951. Methods and results of studies on heterothallism and hybridization in *Tilletia caries* and *T. foetida*. Phytopathology 41:511-521.
10. Lambat, A. K., Nath, R., Mukewar, P. M., Majumdar, A., Rani, I., Kaur, P., Varshney, J. L., Agarwal, P. C., Khetarpal, R. K., and Dev, U. 1983. International spread of Karnal bunt of wheat. Phytopathol. Mediterr. 22:213-214.
11. Large, E. C. 1954. Growth stages in cereals. Illustration of the Feekes scale. Plant Pathol. 3:128-129.
12. Locke, C. M., and Watson, A. J. 1955. Foreign plant diseases intercepted in quarantine inspection. Plant Dis. Rep. 39:518.
13. Matsumoto, T. T., Boratynski, T. N., Showers, D. W., Higuera, D., and Luscher, D. 1984. Karnal bunt of wheat. Calif. Plant Pest Dis. Rep. 3(3):45-47.
14. Matsumoto, T. T., Whitney, N. G., Bonde, M. R., and Royer, M. H. 1985. Morphological variation of teliospores of *Neovossia horrida*. (Abstr.) Phytopathology 75:1365.
15. Mitra, M. 1931. A new bunt of wheat in India. Ann. Appl. Biol. 18:178-179.
16. Morrow, L. A., and Stahlman, P. W. 1984. The history and distribution of downy brome (*Bromus tectorum*) in North America. Weed Sci. 32:(suppl. 1):2-6.
17. Munjal, R. L. 1975. Status of Karnal bunt (*Neovossia indica*) of wheat in northern India during 1968–1969 and 1969–1970. Indian J. Mycol. Plant Pathol. 5:185-187.
18. Peterson, G. L., Bonde, M. R., Dowler, W. M., and Royer, M. H. 1984. Morphological comparisons of *Tilletia indica* (Mitra) from India and Mexico. (Abstr.) Phytopathology 74:757.
19. Royer, M. H., and Rytter, J. 1985. Artificial inoculation of wheat with *Tilletia indica* from Mexico and India. Plant Dis. 69:317-319.
20. Rydrych, D. J. 1983. Jointed goatgrass—a new weed invader (*Triticum cylindricum*). Pages 18-19 in: Columbia Basin Agric. Res. Rep. 680.
21. Singh, R. A., Whitehead, M. D., and Pavgi, M. S. 1979. Taxonomy of *Neovossia horrida* (Ustilaginales). Sydowia 32:305-308.
22. Takahashi, Y. 1896. On *Ustilago virens* Cooke and a new species of *Tilletia* parasitic on rice plant. Bot. Mag. Tokyo 10:16-20.
23. Terrell, E. E. 1977. National List of Scientific Plant Names. Vol. 1. U.S. Soil Conserv. Serv. Agric. Handb. SCS-TP-159. 416 pp.
24. Terrell, E. E., Hill, S. R., Wiersema, J. H., and Rice, W. E. 1986. A Checklist of Names of 3,000 Vascular Plants of Economic Importance. U.S. Dep. Agric. Agric. Res. Serv. Agric. Handb. 505. 241 pp.
25. Tullis, E. C., and Johnson, A. G. 1952. Synonomy of *Tilletia horrida* and *Neovossia barclayana*. Mycologia 44:773-788.
26. Waines, J. G., Hiku, K., and Sharma, H. C. 1982. Species formation in *Aegilops* and *Triticum*. Pages 89-109 in: Grasses and Grasslands: Systematics and Ecology. J. R. Estes, R. J. Tyle, and J. N. Baunken, eds. University of Oklahoma Press, Norman. 312 pp.
27. Warham, E. J., Mujeeb-Kazi, A., and Rosas, V. 1986. Karnal bunt (*Tilletia indica*) resistance screening of *Aegilops* species and their practical utilization for *Triticum aestivum* improvement. Can. J. Plant Pathol. 8:65-70.
28. Whitney, N. G., and Frederiksen, R. A. 1971. Kernel smut of rice. Pages 131-132 in: Proc. Annu. Tex. Conf. Insect Plant Dis. Weed Brush Control 4th.
29. Whitney, N. G., and Frederiksen, R. A. 1975. Kernel smut of rice. Tex. Agric. Exp. Stn. Bull. MP 1231. 12 pp.