Occurrence of *Typhula* species and Observations on Numbers of Sclerotia in Soil in Winter Wheat Fields in Washington and Idaho

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This article is based on part of a Ph. D. dissertation by the first author.
Scientific Paper 7161, Project 0562, College of Agriculture and Home Economics, Washington State University, Pullman 99164.
Accepted for publication 26 September 1985 (submitted for electronic processing).

ABSTRACT

Jacobs, D. L., and Bruehl, G. W. 1986. Occurrence of *Typhula* species and observations on numbers of sclerotia in soil in winter wheat fields in Washington and Idaho. Phytopathology 76:278-282.

Typhula incarnata developed over a wider geographic area than *T. idahoensis* or *T. ishikariensis*, had a competitive advantage in attacking crown and root tissues of wheat (*Triticum aestivum*) beneath the soil surface, and was relatively prevalent in areas or seasons unfavorable for development of snow mold, 1980–1983. When conditions favored snow mold, *T. idahoensis* and *T. ishikariensis* occurred more frequently on leaves than did *T. incarnata*. As many as 670 total (germinable plus ungerminable) sclerotia per kilogram of dry field soil were found in one site in Oneida County, ID, but populations greater than 450 total sclerotia per kilogram were unusual. Under conditions favoring snow mold, 60–70 germinable sclerotia per kilogram of soil produced near maximum disease severity. Disease severity was positively correlated with a logarithmic increase in inoculum density. Germination of sclerotia incubated on potato-dextrose agar averaged 57% for sclerotia newly formed on winter wheat and 46% for sclerotia of unknown age screened from soil, suggesting that some form of endogenous dormancy is present.

Typhula snow molds of winter wheat (*Triticum aestivum* L.) which destroy leaves are limited to areas and seasons in which snow cover persists for 100 days or more on unfrozen or lightly frozen soil (13). *Typhula idahoensis* Remsberg and *T. ishikariensis* Imai are limited to these conditions, but *T. incarnata* Lasch ex Fries occurs in both snow mold areas (1,2,7,12,13) and peripheral areas in which snow cover is limited (8). *T. incarnata* attacks roots and crowns of winter cereals under conditions unsuited for *T. idahoensis* and *T. ishikariensis*, resulting in its broader geographic distribution (8,10,12). *T. incarnata*, under deep and prolonged snow cover, is less virulent than the other two species (1,6).

Early studies (2,4) did not determine the relative quantitative distribution of *T. idahoensis* and *T. ishikariensis*. Bruehl and Machtmes (4) identified sclerotia that were free of host tissue obtained from herbarium specimens collected over a period of years in Idaho and Washington. Sclerotia of *T. idahoensis* are usually embedded within host tissues while many sclerotia of *T. ishikariensis* are borne superficially on leaves and dislodge easily. Therefore, Bruehl and Machtmes (4) cautioned that the totals reported did not reflect the true relative numbers of the two species. Selecting sclerotia free of host tissue favored isolation of *T. ishikariensis*.

In the present study, sclerotia were screened from field soil to obtain unbiased information on the relative distribution of the three species in Wáshington and Idaho, to determine the number of sclerotia present per kilogram of field soil, and to establish the relationship between the numbers of germinable sclerotia in soil and the severity of snow mold.

MATERIALS AND METHODS

Soil samples were collected in winter wheat, summer-fallow regions of Washington in 1980, 1981, and 1983 and in Idaho in 1982. Samples were obtained either when wheat was growing (the crop year) or in fallow soil following winter wheat. Soil was collected with a shovel from the surface 5 cm; small quantities were obtained at 1.5 m-intervals until the quantity per sample exceeded 10 kg of dry soil. Wheat in local dryland, summer fallow regions is seeded with deep-furrow drills in rows 40 cm apart. When wheat was present, the soil samples were taken from between the rows so that the presence of wheat at the time of sampling had no effect upon sclerotial numbers in the soil sample and no newly-formed sclerotia were obtained: all sclerotia subsequently recovered from these samples were residual sclerotia from previous wheat crops. After collection, the soil was screened through a 6-mm-mesh screen to remove coarse debris, mixed, air dried, and stored in the laboratory.

Recovery of sclerotia from soil samples. Sclerotia were obtained from each soil sample by wet sieving four 500-g samples through screens with sieve sizes of 1,000, 710, 500, and 300 μm. The sclerotia are more dense than water. The material remaining on each screen was washed with a wash bottle into glass petri dishes. As many dishes as required to obtain a shallow layer of sand and sclerotia in each dish to facilitate visual examination were used. Sclerotia, observed through a dissecting microscope, were removed from the sand in the dishes with forceps and transferred to a separate dish containing water. When all sclerotia had been removed, water was drawn from the collection dish with a pasteur pipette and the sclerotia were air dried for 3–6 mo in the laboratory at 20 C. The sclerotia in the collection dish from each sieve were counted and handled separately for each sample.

Sclerotia were surface-disinfested for 60 sec in a solution of 0.525% sodium hypochlorite containing one drop of liquid detergent per 100 ml of solution. The solution was changed every 20 min. Four disinfested sclerotia were placed on each petri dish of potato-dextrose agar (PDA) and incubated at 10 C for 4-6 wk. As germination occurred, hyphae were transferred to individual dishes of PDA. Cultures were identified by mating the unknown dikaryon with tester monokaryons (C-1-48 = ATCC 44102 and 70-22-26 = ATCC 44144) of *T. idahoensis* (3,5). The percent of sclerotia that germinated within each sample was recorded.

Disease development from sclerotia in soil samples. Clay pots 15 cm in diameter were partially filled with Palouse silt loam mixed 1:1 with river sand on top of which was spread 300 cm^3 of sample soil to provide a 2.5–3.0 cm layer of test soil in each pot. Pots containing only the Palouse silt loam sand mix served as controls. Cultivar Daws winter wheat was seeded in these pots in mid-to-late September of each year with 8–10 plants per pot. They were incubated outdoors in sand beds until early December for winter hardening. In December, moist absorbent cotton was placed firmly

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over the plants and the pots were placed at 1 C in the dark in snow mold incubation chambers for 110 days. The cotton was kept moist by occasionally spraying it with water. Each treatment was replicated 10 times.

Disease ratings were determined 20 days after the plants were transferred from the incubation chambers to greenhouse benches under natural daylight at 15–20 C. The disease ratings were determined on a 0–4 rating scale as follows: 0 = no sclerotia, plants vigorous; 1 = few sclerotia, plants vigorous, outer leaf sheath necrotic; 2 = moderate number of sclerotia, plants vigorous, some inner leaf sheaths necrotic; 3 = large number of sclerotia, plants recovering, crowns necrotic; and 4 = large number of sclerotia, plants not recovering, severe necrosis of the crowns.

Leaves, crowns, and roots were sampled randomly and air-dried. One or 2 mo later, sclerotia from these plant parts were surface sterilized, germinated, and mated with tester monokaryons for species identification. The germination of sclerotia was recorded.

Field plant samples. In April 1981, 1982, and 1983, winter wheat was sampled randomly from collection sites in Washington. Each plant sample was obtained from the same area of the field from which soil samples had been collected the previous September. Plants were collected at approximately 1.5-m intervals until a 30- to 40-plant sample was obtained from each collection site. Plants were placed in plastic bags and kept cool.

Twenty plants of each sample were rated for disease severity based on the 0–4 scale. After being rated for disease severity, leaf and crown tissues bearing sclerotia were air-dried and the sclerotia were removed with forceps. The sclerotia were subsequently surface sterilized, germinated on PDA, and mated for identification with tester monokaryons as described above.

RESULTS

Occurence of *Typhula* spp. in soil samples. *T. incarnata* was more widespread and abundant than *T. ishikariensis* or *T. idahoensis* in Washington from September 1980 to April 1983. *T. incarnata* was most abundant in Adams and Lincoln Counties, WA, outside the area in which snow cover normally persists for long periods (Table 1), and in areas in which the preceding seasons were unfavorable to snow mold. *T. idahoensis* dominated in areas of chronic snow mold where it was favored in preceding seasons (in Teton, Franklin, and Oneida Counties, ID). *T. ishikariensis* was recovered in small quantities from soil in five counties.

The exact size of the sclerotia was not determined, but those that passed through the 1,000-μm-mesh screen and were retained by the 710-μm-mesh screen were assumed to have an average diameter of 850 μm. The same method was used to estimate the size of those that passed through other screens. By this rough method, sclerotia of *T. incarnata* averaged 532 μm; those of *T. idahoensis*, 450 μm; and those of *T. ishikariensis*, 436 μm in diameter. No sclerotia were retained on the 1,000 μm screen. Many (about 650) sclerotia of *T. incarnata* were retained by 710-μm screen, 2,789 by the 500-μm screen, and 3,124 by the 300 μm screen. For *T. idahoensis*, 60 were retained on the 710-μm screen, 1,025 by the 500-μm screen, and 3,612 by the 300-μm screen. For *T. ishikariensis*, all passed the 710-μm screen, 36 were retained by the 500-μm screen, and 168 by the 300-μm screen.

Germination of sclerotia. The percent germination of all sclerotia, whether screened from soil or taken from wheat plants from the field or taken from plants attacked in the snow mold chambers, was nearly the same. Germination of 9,134 sclerotia of all three species (total) recovered from field soil was 46%, of 1,765 sclerotia recovered from field-grown plants was 56%, and of 6,587 sclerotia recovered from plants incubated with soil samples in the snow mold chambers was 58%. Considerable variation in germination of sclerotia from site-to-site and within sites occurred.

Disease relative to sclerotial numbers in soil samples. Disease increased rapidly in relation to the number of viable sclerotia in the soil from very low populations to about 60 germinable sclerotia per kilogram, after which it increased less rapidly (Fig. 1). The highest number of germinable sclerotia, 300 per kilogram of air-dried soil, occurred in Idaho. The greatest number found in a field in Washington was 210 per kilogram of air-dried soil. Disease increased linearly with logarithmic increases in numbers of germinable sclerotia (Fig. 2).

Data from wheat fields in Washington are not presented because in most sites in most years environmental conditions did not favor snow mold; therefore, disease was not correlated with inoculum density.

Sclerotia from plants incubated with soil samples. *T. incarnata* was the only species recovered from plants grown in snow mold chambers in the soils from Adams and Lincoln Counties, WA (Table 2). It was the most abundant species on root and crown tissues from all soils, which is evidence of its great advantage below the soil surface. A total of 1,299 sclerotia of *T. incarnata* were recovered from leaves and 634 from the crowns and roots, a 2:1 ratio of leaves to crowns and roots. The ratio of sclerotia on leaves versus those on crowns and roots was 22:1 (517:24) for *T. idahoensis* and 24:1 (119:5) for *T. ishikariensis*. *T. ishikariensis* occurred on leaves of wheat plants grown in samples from Spokane and Stevens Counties, WA. *T. idahoensis* was most abundant on samples from Okanogan County, WA, and on all leaf samples from Idaho. *T. idahoensis* and *T. ishikariensis* increased relative to *T. incarnata* in every soil in which they were present, which is evidence of their competitive advantage under conditions favoring true snow mold (Table 3).

Sclerotia on plants from Washington fields. Conditions in all but Okanogan County were unfavorable to snow mold in 1981 and 1982 and *T. incarnata* predominated (Table 4). Conditions were somewhat more favorable in Okanogan County than other counties and *T. idahoensis* was isolated from a high percentage of plants. In 1983, snow mold was favored in Okanogan and Douglas Counties and *T. idahoensis* increased. In the summer-fallow system, the sites sampled in 1981 and 1983 were the same. *T.*

TABLE 1. Distribution of *Typhula* spp. as determined from germinable sclerotia screened from wheat-field soil in Idaho and Washington, 1980–1983

State County	Number of sites	Number identified	Species (%)		
			T. incarnata	*T. idahoensis*	*T. ishikariensis*
Washington					
Adams	4	174	100	0	0
Lincoln	3	216	99	1	0
Stevens	3	289	93	0	7
Spokane	2	152	91	0	9
Douglas	7	1,384	62	35	4
Okanogan	4	468	62	35	4
Idaho					
Camas	4	270	47	52	1
Teton	7	215	29	71	0
Franklin	7	235	14	86	0
Oneida	6	342	4	89	7
Average			61	36	3

idahoensis increased from 4% in 1981 to 64% in 1983 in Douglas County and from 26 to 46% in Okanogan County, showing a shift in population in response to a season favoring snow mold.

DISCUSSION

The ability of *T. incarnata* to reproduce under conditions unfavorable to either *T. idahoensis* or *T. ishikariensis* and its advantage below the soil surface contribute to its wide geographic distribution and to its ability to grow over a higher temperature range (7). All three species grow at 0 C or below. *T. incarnata* colonized more buried green leaves than the other species (*unpublished*), which is further evidence of its relative advantage below the soil surface. The ability to develop in cool, moist, well aerated soil lessens its dependence upon snow cover for conditions favorable to pathogenesis and extends its geographic range to areas in which *T. idahoensis* and *T. ishikariensis* cannot persist.

At sample sites in Washington, the proportion of *Typhula* species changed from year to year. The abundance of *T. incarnata* in soil and on leaves relative to the other species reflects the number of seasons unfavorable to the more aggressive species. Favorable conditions for snow mold during the winter of 1982–1983 in Okanogan and Douglas Counties were responsible for the greater frequency of sclerotia of *T. idahoensis* than of *T. incarnata* collected from both soil and plants from those counties in 1983. The percentage of sclerotia of *T. idahoensis* isolated from soil in Douglas County in September 1981 was 19%, but the percentage isolated from the same sites in September 1983 was 51%. A similar relationship occurred with sclerotia isolated from naturally infected plants (Table 3). In seasons with deep snow favorable for the leaf blight phase of snow mold, *T. idahoensis* and *T. ishikariensis* were isolated more frequently than was *T. incarnata*. In southern Idaho, after several seasons favorable to snow mold, *T. idahoensis* was the most abundant species, especially in soils from Oneida County (Table 1). In every case, when soil collected from the field contained *T. idahoensis* and/or *T. ishikariensis*, and wheat

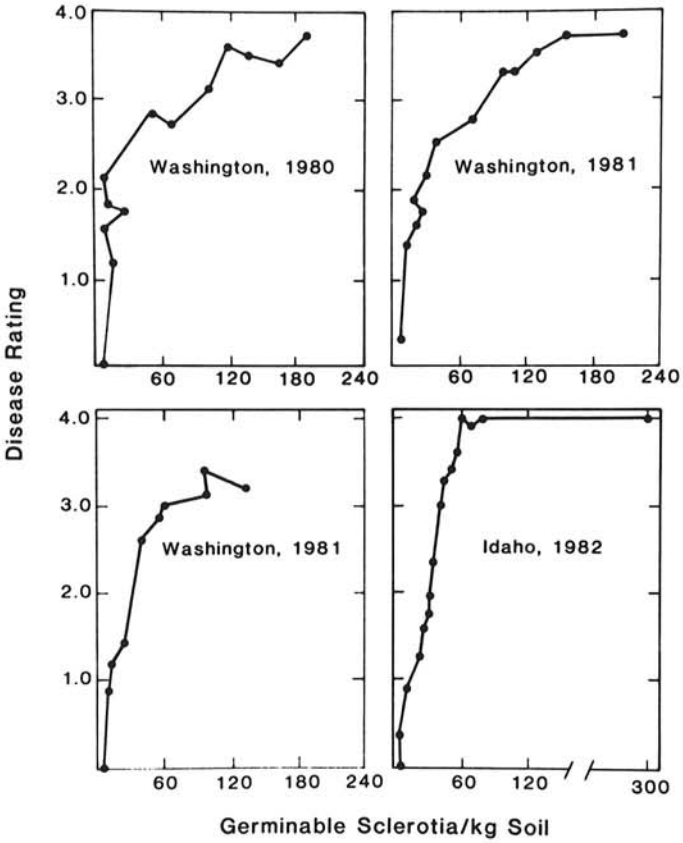

Fig. 1. The influence of inoculum density of sclerotia of *Typhula* spp. in soils collected in Washington and Idaho upon disease severity of winter wheat incubated under controlled conditions. Two sets of data are presented for Washington 1981 from collections made in September, so that all fields (fallow or in wheat) were sampled.

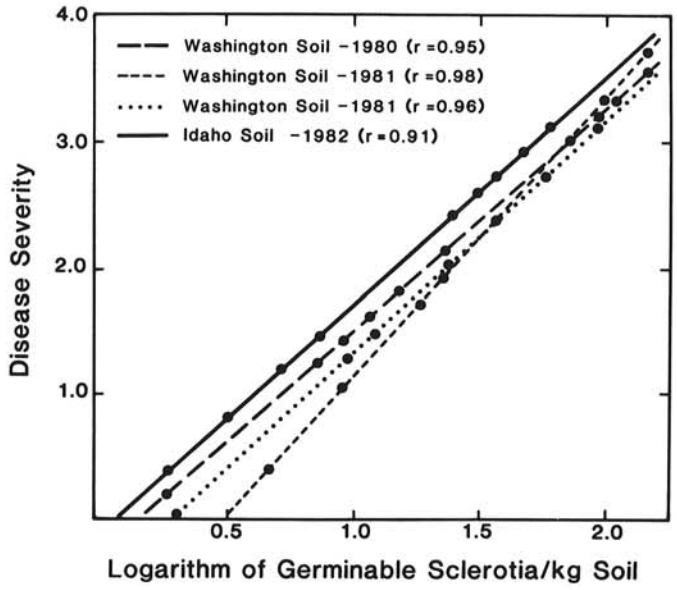

Fig. 2. Disease severity in winter wheat under conditions favorable to snow mold increased linearly with the logarithmic increase in the number of sclerotia of *Typhula* spp. germinable on PDA per kilogram of field soil.

TABLE 2. Identification of *Typhula* spp. on winter wheat plants grown in soil collected in various parts of Washington and Idaho after incubation under conditions favorable to Typhula snow mold

State / County	Number identified	From leaves (%)			Number identified	From crowns and roots (%)		
		inc[a]	*ida*	*ish*		*inc*	*ida*	*ish*
Washington								
Adams	280	100	0	0	88	10	0	0
Lincoln	258	100	0	0	83	100	0	0
Stevens	244	78	0	22	74	95	0	5
Spokane	193	76	0	24	35	98	0	2
Douglas	709	54	46	0	325	93	7	0
Okanogan	191	17	75	7	58	96	2	0
Idaho								
Camas	268	12	86	2	62	90	10	0
Teton	205	7	93	0	3	100	0	0
Franklin	201	4	96	0	7	100	0	0
Oneida	337	1	94	5	0			
Average		45	49	6		97	2	1

[a] Abbreviations: *inc* = *T. incarnata*, *ida* = *T. idahoensis*, and *ish* = *T. ishikariensis*.

TABLE 3. Shift in percent of sclerotia of *Typhula idahoensis* + *T. ishikariensis* relative to those of *T. incarnata* in original soil samples and on wheat plants after one cycle of disease

State County	(*T. ida*[a] + *T. ish*) − *T. inc*		
	Originally in the soil (%)	On plants after 1 cycle (%)	Increase (×)
Washington			
Stevens	7	18	2.6
Spokane	9	21	2.3
Douglas	25	34	1.4
Okanogan	39	64	1.6
Idaho			
Camas	53	73	1.4
Teton	71	92	1.3
Franklin	86	93	1.1
Oneida	89	99	1.1

[a] Abbreviations: *ida* = *idahoensis*, *ish* = *ishikariensis*, and *inc* = *incarnata*.

TABLE 4. Identification of sclerotia of *Typhula* spp. collected from naturally diseased wheat plants in Washington, 1981–1983

County	Number of sites	Date	Number identified	Typhula spp. (%)		
				inc[c]	*ida*	*ish*
Adams	2	1981	27	100	0	0
	2	1982	67	100	0	0
Lincoln	2	1981	7	100	0	0
	1	1982	55	100	0	0
Spokane	1	1981	12	100	0	0
	1	1982	22	96	0	4
Douglas	4	1981	154	96	4	0
	3	1982	175	93	7	0
	4	1983	238	36	64	0
Okanogan	2	1981	47	76	26	0
	2	1982	51	82	18	0
	2	1983	112	50	46	4

[a] Abbreviations: *inc* = *T. incarnata*, *ida* = *T. idahoenis*, and *ish* = *T. ishikariensis*.

grown in this soil was incubated in the snow mold chambers, the relative isolation of *T. incarnata* diminished (Table 3). It is to be expected, conversely, that after seasons relatively unfavorable to snow mold, the relative proportion of *T. incarnata* in the population would increase. In an earlier period of years (2), *T. ishikariensis* was abundant in Stevens and in northern Spokane Counties, WA, but during the years of these studies it was relatively rare (Table 1). The relative prevalence of these species changes rapidly in response to winter conditions.

This study did not explain the importance of *T. idahoensis* in Douglas and Okanogan Counties, WA, and in Idaho relative to *T. ishikariensis* (Table 1). After an earlier series of winters favorable to both species, *T. idahoensis* was important in snow mold regions which were previously grasslands and which have 25–33 cm annual precipitation, 10 cm of which was usually snow (2). In snow mold areas with greater than 40 cm annual precipitation and much snow on former forested land, *T. ishikariensis* was important (2). In Washington, most of the winter wheat subject to *T. idahoensis* is grown at or slightly below 900 m elevation. In southern Idaho, where *T. idahoensis* is dominant, most of the wheat is grown at elevations between 1500 and 1800 m. We have no average light intensity figures for November for the various areas, but we suspect that light intensity increases with elevation. In Hokkaido, Japan, Matsumoto and Sato (11) found that *T. idahoensis* was associated with areas with more intense sunlight in autumn, while *T. ishikariensis* was associated with areas of heavier snow fall and less intense autumn sunlight. They found that *T. idahoensis* was more virulent on fully hardened wheat plants than was *T. ishikariensis*. It is possible that wheat is more hardened prior to winter on the former grasslands than in the regions of former forests in Washington and Idaho, and that Matsumoto and Sato (11) have discovered a significant factor in the ecology of these two species.

Analysis of the relative species composition of the Typhula complex in nature is accomplished most accurately by enumerating sclerotia obtained from soil. The earlier survey based on sclerotia free within collection envelopes (4) was biased toward *T. ishikariensis* rather than *T. idahoensis* as predicted. Also, it is difficult to make truly random plant samples by visual selection. Big sclerotia, tiny sclerotia, shape, or color variants are difficult to ignore. They will more likely than not find their way into the sample. Sclerotia sieved from the soil are sampled without bias by either conscious or unconscious selection.

Endogenous dormancy within sclerotia produced on host tissue is important, especially for *T. idahoensis* and *T. ishikariensis*. Weather conditions every autumn and every spring provide periods of temperature, oxygen, and moisture capable of inducing germination. If all sclerotia in the surface 2-3 cm of soil germinated in a year unfavorable to mold, the pathogens would decline precipitously. In the summer-fallow system, with wheat planted once every 2 yr, attrition could lead to near extinction with two or more unfavorable seasons in succession.

Huber and McKay (9) reported 97% germination of field sclerotia of *T. idahoensis* on cornmeal-dextrose agar at 10 C. The sclerotia were from diseased wheat from southern Idaho. In that survival study, few sclerotia disintegrated after burial in soil, even though many would no longer germinate. In our study, the percent germination of sclerotia recently formed on naturally infected winter wheat and winter wheat incubated in environmental chambers was 56 and 58%, respectively, while that of sclerotia of unknown age screened from soil was 46%. The similar percent germination of sclerotia of different ages indicates that some type of endogenous dormancy mechanism contributes to the prevention of sclerotial germination. We do not know how many sclerotia that did not germinate in our studies were dead, but the fact that germination of new sclerotia from wheat plants was only about 10% greater than the average of those screened from soil gives us no reason to believe they were dead.

Davidson and Bruehl (6) reported that 300 sclerotia of *T. idahoensis* randomly mixed within 1 kg of field soil produced near maximum disease. The sclerotia of their study were collected from diseased wheat in Camas County, ID. The 300 were the total number of sclerotia in the soil. Germination of that collection on washed river sand averaged 32% and on acidified corn meal agar, 80%. The 300 sclerotia per kilogram of soil is equivalent to 96 sclerotia per kilogram that germinated without exogenous food on sand or 240 that germinated on agar media. All numbers involving disease development in the present study are based on sclerotia germinable on PDA.

In our study, fewer than 15 germinable sclerotia per kilogram of dry soil resulted in detectable disease under favorable conditions and maximum severity was reached with 70–100 germinable sclerotia per kilogram in Washington soil samples and with 50 germinable sclerotia per kilogram in Idaho soils. The lower inoculum density required to produce maximum disease on plants grown in soils from Idaho than on plants grown in soils from Washington may be due to the greater proportion of *T. idahoensis* in soils from Idaho. *T. idahoensis* is more virulent on winter wheat than is *T. incarnata* (2,11).

Many variables contribute to the problem of determining the number of sclerotia required per volume of soil to produce a given amount of disease. Only sclerotia of *T. idahoensis* located on or near the soil surface (within the top 2 cm) are effective in initiating infection (6). Fewer sclerotia are probably required when many large leaves from early-seeded wheat contact much of the soil surface. How many sclerotia actually germinate in nature? The 32% germination on river sand and the 80% germination of sclerotia of the same collection on laboratory medium (6) makes one wonder how many actually germinated in and on the soil in the present study? A leaf pressed upon a sclerotium by deep snow may leak nutrients and stimulate germination of that sclerotium.

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