Typhula Species Pathogenic to Wheat in the Pacific Northwest

G. W. Bruehl and B. M. Cunfer

Professor, Department of Plant Pathology, Washington State University, Pullman, Washington 99163, and Assistant Professor, Department of Plant Pathology, University of Georgia, College of Agriculture Experiment Stations, Georgia Station, Experiment, Georgia 30212.

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ABSTRACT

Typhula spp. parasitizing wheat can be identified if several morphological characters are used. *T. incarnata* can be identified by its reddish-brown sclerotia and pink basidiocarps, usually by the shape of its basidiospores, and by occasional digitate cells in the sclerotial rind. It is difficult to distinguish *T. idahoensis* from *T. ishikariensis*, both of which have black sclerotia. The basidiocarps of *T. idahoensis* are smaller than those of *T. ishikariensis*, and the fertile heads are brownish rather than whitish. The size and shape of basidiospores of different collections of the two species are similar, so spores are not diagnostic. Sclerotia of *T. idahoensis* are less globose and more frequently borne within host tissues, and the rind cell patterns are more irregular than those of *T. ishikariensis*.

Typhula incarnata is the least virulent on all hosts. *T. idahoensis* is virulent on winter cereals and some grasses, but on few dicotyledonous species. *T. ishikariensis* is virulent on winter cereals, grasses, legumes, and many other dicotyledonous species. *T. incarnata* thrives on early-seeded winter cereals throughout the northern half of eastern Washington, whereas *T. idahoensis* and *T. ishikariensis* are restricted to areas of frequent prolonged snow cover. *T. idahoensis* is dominant on former grasslands or grass-sagebrush lands; *T. ishikariensis* is dominant on former forest lands.

Light intensity within plant refuse may be less than 10 percent of unimpeded light. Because variation in basidiocarp size and color results from low light intensity, only basidiocarps which have matured in full light should be used for species diagnosis.

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Since 1969 *Typhula* spp. pathogenic to winter wheat (*Triticum aestivum* L.) have been tentatively assigned to three species; *T. incarnata* Lasch ex Fries with reddish-brown sclerotia and pink basidiocarps, *T. idahoensis* Remsberg with black sclerotia and tan-brownish basidiocarps, and *T. ishikariensis* Imai with black sclerotia and powdery white to watery gray basidiocarps. Observation of sclerotial rind patterns and basidiocarps led us to accept the validity of these species, but similarities between *T. idahoensis* and *T. ishikariensis*, which some authors placed in synonymy (10, 13), were so great, we withheld publication of this paper on their morphology, physiology, and ecology until mating experiments established the degree of compatibility among them.

Neither *Typhula trifolii* Rostrop nor *T. incarnata* (4) mated with any other of our species; some monokaryons of *T. idahoensis* and *T. ishikariensis* exchanged nuclei, but the products of these unions were essentially sterile (2). Because of this high degree of genetic separation, we accept all the above-mentioned species, and present this paper.

MORPHOLOGY.—*Sclerotia.*—Sclerotia found on diseased or dead plant parts in late winter and early spring are often the most important structure of diagnosis (14). Sclerotia are lighter in color when immature, and we refer to the color of mature, dry sclerotia as seen by the unaided eye. Sclerotium size varies with the plant structure colonized, the duration of conditions favoring mold, and the extent of dehydration. Jamalainen (9) noted that herbarium specimens of *Sclerotinia borealis* were smaller than recent field collections, and he attributed the discrepancy to continued desiccation.

The reddish-brown sclerotia of *T. incarnata* are 1-3 mm in diameter when formed below the soil surface among leaf sheaths or on roots; they are usually half that size or less when formed on leaf blades upon the soil surface. The black sclerotia of *T. idahoensis* are slightly larger (the average dimensions of 120 sclerotia of three collections was 0.81 × 0.63 mm), less globose, and more of them were formed sub-epidermally than sclerotia of *T. ishikariensis* (140 sclerotia of four collections averaged 0.63 × 0.54 mm). If sclerotia of *T. idahoensis* form superficially they too are quite globose. The nearly spherical sclerotia of *T. ishikariensis* are usually produced superficially on leaves and are easily dislodged. Sclerotia of *T. idahoensis*, *T. ishikariensis*, and *T. incarnata* may form in rotted tissues below ground.

Rind cell patterns.—Remsberg (14) emphasized the diagnostic value of rind cell patterns of mature sclerotia. Patterns of sclerotia produced in culture and on wheat of at least eight isolates of each species were examined. Dried sclerotia were soaked in water for at least 2 hours, rind fragments removed under a dissecting microscope with new razor blades, and mounted in lacto-phenol on glass slides. These injured sclerotia may be surface disinfected in a (1:1, v/v) mixture of ethyl alcohol and 5.25% sodium hypochlorite solution and plated on agar media. Generally, a greater number of wounded sclerotia will germinate than will comparable nonwounded sclerotia.

The cell patterns of sclerotia produced on laboratory media and on the host were alike, confirming Koske's (11) observation that the rind pattern of *T. erythropus* did not

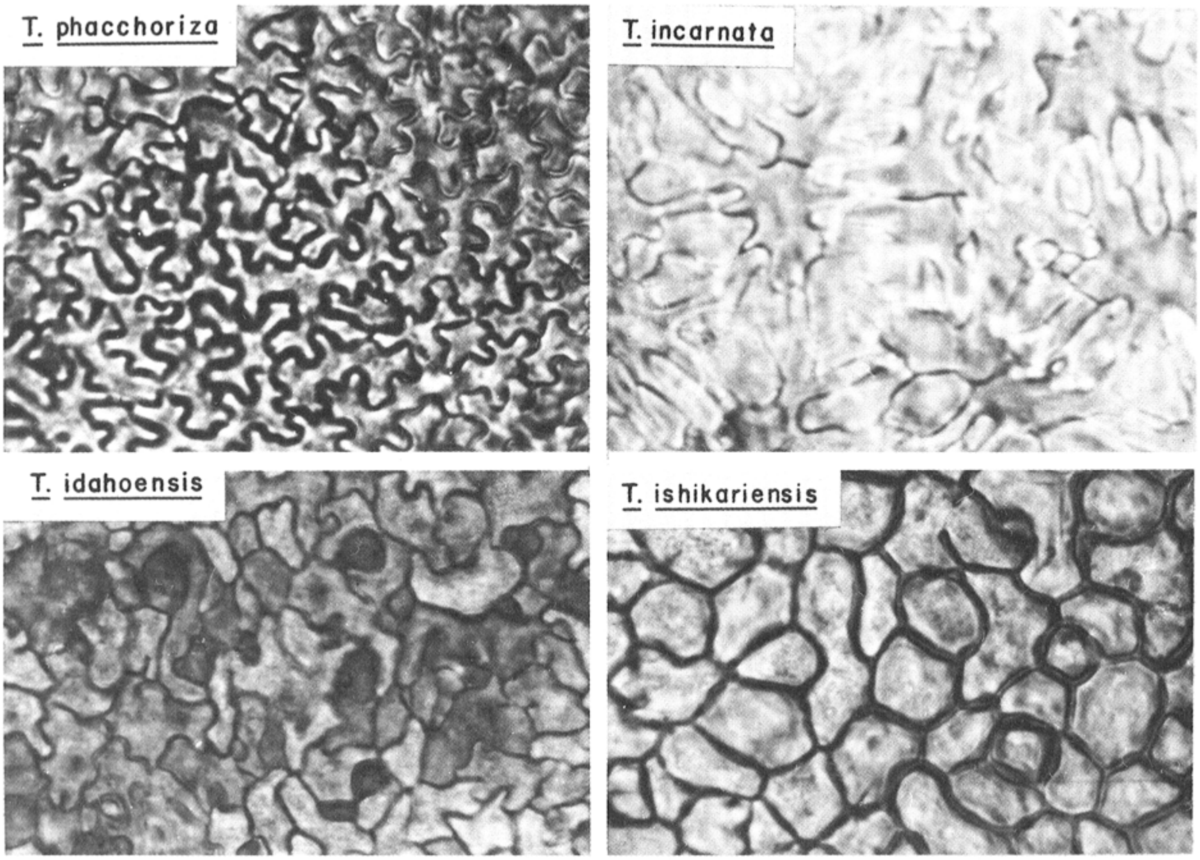

Fig. 1. Sclerotial rind fragments of *Typhula phacchoriza*; *T. incarnata* with radiate cells; *T. idahoensis*; and *T. ishikariensis*.

vary significantly with conditions of growth. Rind patterns among isolates of a species are variable, but rinds are probably of greater diagnostic value than most other characters. Radiate or digitate cells are occasionally found among the irregular cells of *T. incarnata* (Fig. 1). The radiate cells are infrequent and several fragments may have to be examined to find them. The rind pattern of *T. idahoensis* is irregular (14). There are many partially broken cells that appear to have separated during maturation of the sclerotium (Fig. 1). The rind pattern of *T. ishikariensis* is regular [see Fig. 6-A of Ylimäki (20)] and the corners of the cells are sharper than those of *T. idahoensis* (Fig. 1). Rinds of *T. ishikariensis* are easier to remove and frequently come off in a layer one-cell thick. The rind pattern of *T. phacchoriza*, which is nonpathogenic, is essentially constant (Fig. 1) in all isolates we observed, but the size of the cells varies from collection to collection.

Scanning electron micrographs showed that the sclerotial rinds of all three species were covered by amorphous substances that obscured the cell patterns (Fig. 2).

Basidiocarps.—To minimize variations arising from environmental conditions (5, 12), several isolates were increased on a sand-bran-dextrose medium (3) and placed outdoors on soil in clay pots at Pullman, Washington, in late summer, 1970-1973. The clay pots were sunk in sand beds to reduce soil desiccation. Basidiocarps appeared from late October until cold weather inhibited development.

Typhula incarnata basidiocarps averaged 6.6, *T. ishikariensis* 6.1, and *T. idahoensis* 3.4 mm in total height in 1971 (Table 1). The total range in average height among four isolates of *T. ishikariensis* was 3.9-7.5 mm; among seven isolates of *T. idahoensis* the range was 2.9-3.6 mm. The average heights of basidiocarps, produced under similar conditions, did not overlap. The heights of basidiocarps in moist seasons is considerably greater, but differences in relative size remain.

Basidiocarps of *Typhula incarnata* are always some shade of pink, and are occasionally branched or fasciated. The probasidiocarps of both *T. idahoensis* and *T. ishikariensis* are dark, and the stipes of both remain dark. The fertile heads of *T. idahoensis* are brownish and those of *T. ishikariensis* are white or white-grayish. The heads of *T. ishikariensis* tend to darken with age (8), so that the color of senescent specimens of *T. idahoensis* and *T. ishikariensis* may overlap. Old heads of *T. ishikariensis* tend to become inflated to almost spherical or irregular (18, p. 14). No studies were made of the basidia or sterigmata.

Basidiospores.—Basidiospores were obtained by placing basidiocarps on glass slides and incubating them at 10 C in the dark for 12-24 hours after which they were

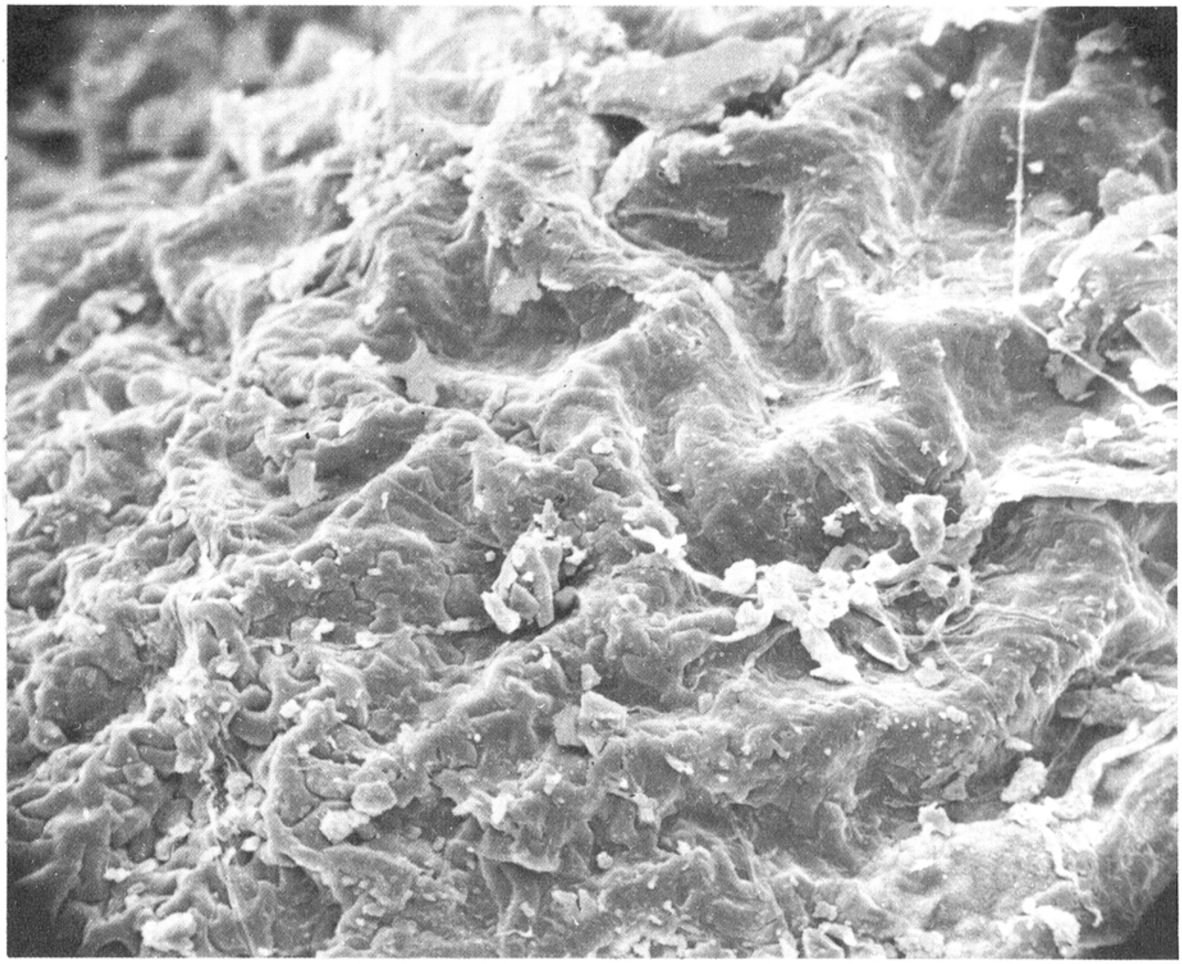

Fig. 2. Scanning electron photomicrograph of the surface of a *Typhula incarnata* sclerotium, × 340. (Picture by L. J. Peterson. University of California, Davis).

mounted in lacto-phenol containing cotton blue. Spore measurements were made with an ocular micrometer or from photographs. Spores of 1-11 individual basidiocarps per isolate were measured, and at least 13 isolates per species were studied (Table 2).

Average measurements made by Ekstrand (6) of *T. incarnata* spores from individual basidiocarps ranged from 3.3 × 7.9 μm for the smallest to 4.0 × 10.3 μm for the largest. We, like Ekstrand, found considerable variation in spore size from culture to culture. Variations within each species were such that spore dimensions in all three species overlapped. The only diagnostic value of basidiospores is the tendency of *T. incarnata* spores to be more rectangular than those of *T. idahoensis* and *T. ishikariensis*.

Our measurements of both basidiocarps and basidiospores are smaller than those reported by other workers (6, 8, 13, 14, 18). We think this is a result of incubation in full sunlight on soil in clay pots, a xerophytic site compared to incubation among stubbles and weeds. In 1971, spores averaged larger than in 1970, the latter being a drier season.

ECOLOGY AND PHYSIOLOGY.—*Distribution.*—*Typhula incarnata* is practically ubiquitous in cultivated soils of the northern half of eastern Washington, reflecting adaptation to a wide range of environmental conditions [(7), and page 144 in (15)]. *T. idahoensis* and *T. ishikariensis* develop only after prolonged snow cover, whereas *T. incarnata* attacks roots and basal crown tissues in the absence of conditions requisite for typical snow mold development.

T. idahoensis is the dominant species on winter cereals grown on former grasslands or grass and sagebrush (*Artemesia* spp.) associations in areas with annual precipitation between 25-33 cm. Ten centimeters of this is usually in the form of snow. *Typhula idahoensis* has been found in Chelan, Douglas, Grant, Lincoln, and Okanogan Counties, Washington; in Bear Lake, Blaine, Camas, Franklin, Lemhi, Madison, Oneida, Power, and Teton counties, Idaho; in Box Elder County, Utah; and in Flathead County, Montana.

Typhula ishikariensis is the dominant species on winter cereals grown in formerly forested areas, which are usually areas with greater than 40 cm of annual

TABLE 1. Length and width of fertile heads, length of stipes, and total height of basidiocarps of *Typhula* spp. grown outdoors in 1971. Twenty measurements per datum. Note pot-to-pot variation in culture 69-7 of *T. ishikariensis*

Typhula spp. cultures	Fertile head length (mm)	Fertile head width (mm)	Stipe length (mm)	Total height (mm)
T. incarnata[a]				
6316	4.2	0.9	1.5	5.7
6316	5.0	1.0	1.9	6.9
66-9	4.7	1.5	2.5	7.2
66-18	4.2	1.0	1.5	5.7
66-21	5.3	0.9	2.3	7.6
Average	4.7	1.0	1.9	6.6
T. ishikariensis[a]				
69-7	1.7	0.9	2.1	3.9
69-7	4.0	1.3	3.3	7.3
69-7	2.4	0.8	2.7	5.1
70-5	3.1	1.2	2.8	5.9
70-5	3.3	1.0	2.6	5.9
70-11-c	3.7	1.0	2.9	6.7
70-11-d	5.4	1.0	2.2	7.5
70-11-d	4.7	0.9	1.9	6.6
Average	3.5	1.0	2.6	6.1
T. idahoensis[a]				
5999-5	1.7	0.8	1.3	3.0
6258	2.3	0.8	0.9	3.2
6258	2.4	0.7	1.1	3.5
6268	2.0	0.7	1.0	2.9
6274	2.5	0.8	1.2	3.6
70-24	2.3	0.9	1.4	3.7
70-24	2.0	0.9	1.6	3.6
T. ida. 1	1.9	0.5	1.7	3.6
Average	2.1	0.8	1.3	3.4

[a]Basidiocarps produced in autumn, 1973, were considerably larger, but that was one of the wettest falls and winters on record in Washington.

precipitation, much of which occurs as snow. It has been found in Douglas, Okanogan, Spokane, and Stevens counties, Washington; Caribou, Franklin, Lemhi, Teton, and Valley counties, Idaho; and in Flathead County, Montana. The ecological relationships are based largely on observations in Washington because distributions in other states are based on only a few collections, but the few observations in other states substantiate the ecological relationships established in Washington.

Virulence and host range.—Fungal development and sclerotia formation is far greater on winter cereals and green grasses than on straw, stubbles, or dead grass. All three species have limited saprophytic abilities; they are primarily parasites (3).

Typhula idahoensis and *T. incarnata* rarely attack species other than winter cereals and grasses. *T. ishikariensis* attacks green foliage of several legumes and broad-leaved weeds as readily as wheat. Tomiyama (19) reported that *T. ishikariensis* increased more on rape (*Brassica napus* L.) than on wheat in Japan. Ylimäki (20) found that *T. ishikariensis* was most common on clovers in Finland, followed by *T. trifolii* and *T. incarnata*. Because so few plants, other than winter wheat, are green in the autumn in Washington, we did a limited host range study with our isolates.

The fungi were grown on sand-bran-dextrose medium (3) and 40 cm^3 of inoculum were added to the soil surface of each 15.2-cm (6-inch) clay pot containing Alfa alfalfa (*Medicago sativa* L.), Lakeland red clover (*Trifolium pratense* L.), Dwarf Essex rape, or wheat. Hosts were seeded in September and grown outdoors until 25 November 1970, when they were inoculated. Incubation was for 50 days at 0.5 C at 100% RH. *T. incarnata* (12 isolates) was least virulent on all hosts and *T. ishikariensis* (seven isolates) was most widely virulent (Table 3). These results are based on leaf damage alone, thus exaggerating the virulence of *T. idahoensis* (12 isolates) and *T. incarnata* on the dicots. *T. idahoensis* and *T. incarnata* produced few sclerotia on the dicots, and the plants were not killed. In contrast, sclerotia of *T. ishikariensis* formed in abundance, and the plants were killed. Admittedly, the fungal species are not represented by many isolates, but the differences in host range and virulence are probably real.

Water relations.—*Fusarium nivale*, *T. idahoensis*, and *T. incarnata* grow best at high water potentials (1). *T. ishikariensis* was not studied. Because *T. ishikariensis* is found in Washington in areas of higher rainfall than *T. idahoensis*, we studied five isolates of each of the black-sclerotial species in vitro. Potato-dextrose agar (PDA) was adjusted with KCl or sucrose, and incubation was at 0.5 C. Growth was recorded as mycelial diameters after 23 and 30 days. Both species responded equally to water stress (Fig. 3). Direct response to water stress should not affect the distribution of *T. idahoensis* vs. *T. ishikariensis*.

Temperature.—Five isolates each of *T. idahoensis* and of *T. ishikariensis* were incubated on PDA at 0.5, 5, 10, and 15 C. The rates of growth of both were comparable at 0.5 C, the temperature nearest that under snow on unfrozen soil where most growth occurs in nature. At 5 and 10 C, *T. ishikariensis* grew more rapidly than *T. idahoensis*, but at 15 C *T. idahoensis* grew slightly more rapidly than *T. ishikariensis*. The difference in growth rates of *T. idahoensis*, *T. ishikariensis*, and *T. incarnata* is best seen at 10 C and this temperature is recommended for in vitro comparisons. It appears that temperature response to growth under snow does not influence the distribution of *T. idahoensis* and *T. ishikariensis*.

Colony type.—Most isolates of *T. ishikariensis* produced a brown pigment in corn meal agar cultures, but so also did a few isolates of *T. idahoensis*. The pigmentation cannot be used to distinguish the species. Sclerotia of *T. idahoensis* are frequently aggregated in the center of the colony, but those of *T. ishikariensis* are usually single, either scattered or in concentric rings.

Resistance of basidiocarps to drying.—Basidiocarps sporulate after exposure to freezing and desiccation. Mature, sporulating *T. incarnata* basidiocarps were placed on a greenhouse bench for 8 days at 10 C. The withered fruiting bodies were rehydrated in a saturated atmosphere at 10 C for 48 hours, and heavy spore showers occurred. Spores deposited on PDA developed colonies, indicating that some of the spores were viable.

Time of sporulation.—Sprague (15, 16) and Sprague and Rainey (17) noted that during the relatively moist fall of 1951, *T. idahoensis* began sporulating 25 October; and that in the dry autumn of 1952, fruiting began 27 November. When water was not a limiting factor, *T. incarnata* fruited 7 days before either *T. idahoensis* or *T. ishikariensis* at Pullman, Washington. In dry seasons (1969-1971) all three species sporulated about 10-15 November in the field, apparently responding to the fall

TABLE 2. Dimensions (μm) of basidiospores of *Typhula* spp. ejected onto glass slides and preserved in lacto-phenol with cotton blue. Ten and 20 spores per basidiocarp were measured in 1970 and 1971, respectively

	T. incarnata				*T. ishikariensis*				*T. idahoensis*			
Year	Spores per isolate	L[a] (μm)	W[a] (μm)	L/W[a]	Spores per isolate	L[a] (μm)	W[a] (μm)	L/W[a]	Spores per isolate	L[a] (μm)	W[a] (μm)	L/W[a]
1970	40	7.8	2.9	2.7	60	8.0	2.9	2.8	30	7.8	2.6	3.0
	40	8.3	3.6	2.3	10	8.3	2.8	3.0	50	7.5	2.8	2.7
	70	7.4	3.0	2.5	40	8.3	3.0	2.8	40	7.6	2.8	2.7
	20	8.5	3.1	2.7	30	8.1	2.9	2.8	30	6.7	2.6	2.5
	20	8.0	2.8	2.8	10	7.6	2.6	3.0	20	6.5	3.1	2.1
	40	8.1	3.0	2.7	20	8.6	3.7	2.4	20	8.1	2.8	2.9
	60	7.5	2.7	2.8	10	7.8	3.1	2.5	10	7.1	2.9	2.5
					20	8.0	3.0	2.7				
Totals	290				200				200			
Averages		7.8	3.0	2.6		8.1	3.0	2.7		7.4	2.8	2.7
1971	80	7.7	2.9	2.6	20	7.3	2.6	2.8	80	8.4	2.4	3.5
	80	9.1	2.9	3.1	220	8.5	2.9	2.9	80	9.1	2.8	3.3
	60	9.2	3.3	2.8	80	9.8	2.9	3.4	60	8.2	2.7	3.0
	80	8.6	3.2	2.7	60	8.1	2.6	3.1	20	8.6	2.8	3.1
	20	9.6	2.6	3.7	40	7.9	2.9	2.7	80	9.1	2.9	3.1
	80	7.9	2.9	2.7					20	8.8	3.3	2.7
	80	9.1	3.2	2.8					100	9.6	3.0	3.2
									60	8.8	3.0	2.9
Totals	480				420				500			
Averages		8.6	3.0	2.9		8.6	2.8	3.0		8.9	2.8	3.2

[a]L = length, W = width, L/W = ratio, length/width

rains of this region. In Japan, and in the more moist parts of the world, *T. incarnata* usually sporulates about 2 weeks earlier than *T. ishikariensis* (18), probably a reflection of the higher temperature optimum of the former species.

Sporulation of *Typhula* spp. seems to be governed primarily by temperature and moisture, rather than by day length. In Washington, snow comes earlier at Havillah, elevation 1,220 m, than at Kettle Falls, elevation 490 m. The latitudes of the two places are the same so day length is also the same. Regulation of sporulation by day length would require many local ecotypes in the mountainous Pacific Northwest, yet when collections from Idaho, Montana, Utah, and Washington are, incubated at Pullman, sporulation of various collections occurs essentially simultaneously.

TABLE 3. Destruction of foliage (per cent) in five cultivars of winter wheat, Alfa alfalfa, Lakeland red clover, and Dwarf Essex rape by *Typhula* spp. during 50 days at 0.5 C

	Foliage destruction in			
Fungus	Wheat (%)	Alfalfa (%)	Red Clover (%)	Rape (%)
T. idahoensis	95 (60)[a]	65 (12)	73 (12)	63 (12)
T. incarnata	36 (60)	9 (12)	24 (12)	15 (12)
T. ishikariensis	100 (35)	100 (7)	100 (7)	100 (7)

[a]Number in parentheses represents number of pots containing host plants in each datum. Twelve isolates of *T. idahoensis* and *T. incarnata* and seven isolates of *T. ishikariensis* were used.

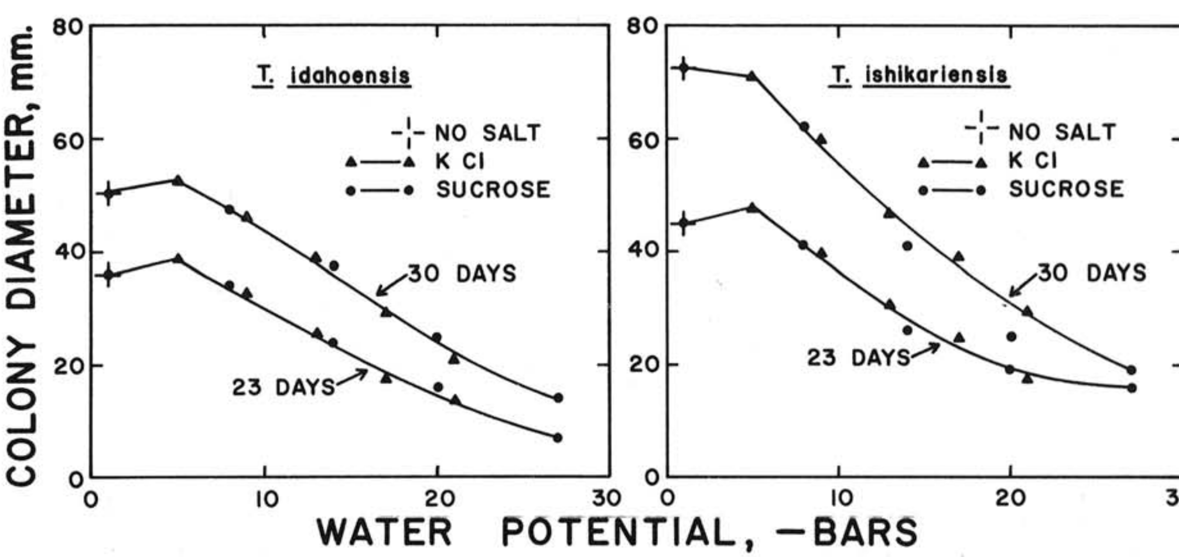

Fig. 3. The influence of water potential upon the in vitro growth of *Typhula idahoensis* and *T. ishikariensis* at 0.5 C. Water potentials reduced by addition of KCl or sucrose to the basal medium.

Influence of light upon basidiocarps.—Use of basidiocarps in taxonomy requires a realization of their response to light as well as to other factors. No fruit bodies of *T. idahoensis* produced with ultraviolet light at 5 C were typical of normal field collections. They were fertile, but etiolated and off-color. Increasing depth of a straw cover from 0-2.5 cm over *T. idahoensis* sclerotia caused them to elongate greatly and change color (5).

Fruit bodies 20-30 mm in height identical to the description of *T. borealis* (6) were found among dense weeds in November 1969. The fungus was isolated, increased, and allowed to sporulate in full light. The basidiocarps produced were only 6-7 mm tall. The fertile heads were white rather than lavendar-tan as when collected in the field, and they were cylindrical rather than tapered, thus fitting the description of *T. ishikariensis* (8). A *Typhula* sp. with fruit bodies 20-40 mm tall, and with whitish-lavender, long, tapered fertile heads was found fruiting among dense leaves near Troy, Idaho. When cultured, it was typical *T. incarnata*. These observations lead us to stress the response of these fungi to light.

We germinated sclerotia on soil in pots with no cover and with one to four layers of coarse cheese cloth. Four layers reduced the light intensity nearly in half, yet this resulted only in slight modification of fruit bodies. Full light on a cloudy November day was 6,728 lux; among dense weeds it was 1,076-1,884 lux, only about one-quarter full intensity. Light on a relatively sunny day was 43,057 lux in wheat stubbles 34-cm tall; light at the soil surface was one-sixth full intensity. Among mixed weeds and stubble it was one-tenth of full light, and we could make no measurements under litter (where many sclerotia germinate) without destroying the litter. In nature, basidiocarps are produced under highly variable light intensities.

DISCUSSION.—Our studies provided no explanation for the apparent advantage of *T. idahoensis* over *T. ishikariensis* on the winter wheat of the more arid areas of Washington. Conditions conducive to the molds incited by these fungi (deep snow on unfrozen or lightly frozen soil) is probably the most uniform and constant physical terrestrial environment in the world (3). Both fungi grow well at near 0 C and both respond to moisture similarly. The broader host range of *T. ishikariensis* could account for its predominance in formerly forested areas. The slightly larger sclerotia of *T. idahoensis* could enable them to withstand greater heat and desiccation. In addition, fewer sclerotia of *T. idahoensis* fall from the dead leaves, thus more of them may be kept from the soil surface. If conditions under deep snow are essentially alike, as we believe, the survival advantage of *T. idahoensis* in more arid regions may depend upon greater over-summering capability (average July precipitation at Waterville, Douglas County, Washington is 1.1 cm; August, 1.0 cm).

Etiolated basidiocarps of *T. ishikariensis* fit the description of basidiocarps of *T. borealis* Ekstrand (6). The brown pigment produced by *T. borealis* in organic agar media and its broad host range (6) further emphasize their similarities. We believe, however, that the two species cannot be accepted as synonymous until mating trial studies of rind patterns of authentic specimens have been made. Under certain conditions of light, age, and moisture, we cannot distinguish with certainity the basidiocarps of *T. idahoensis* from those of *T. ishikariensis*, yet we consider them distinct, and matings between them must be very rare (2).

Although some *Typhula* spp. are difficult to identify, the effort should be made. Species differ in significant ways; in their geographic ranges, host ranges, ecological relations, and in virulence.

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