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Genetic and biological characteristics of *Typhula ishikariensis* isolates from Norway

Naoyuki Matsumoto[1], Anne Marte Tronsmo[2] and Tadayuki Shimanuki[3]
[1]*Department of Environmental Biology, National Institute of Agro-Environmental Sciences, 3-1-1 Kan-non dai, Tsukuba 305, Japan (Fax 0298-38-8199);* [2]*Department of Plant Pathology, Norwegian Plant Protection Institute, Box 70, Ås-NLH, Norway (Present address: Landbrukstilsynet, Postboks 3, N-1430 Ås, Norway);* [3]*Department of Low-temperature Science, Hokkaido National Agricultural Experiment Station, 1 Hitsujigaoka, Toyohira-ku, Sapporo 062, Japan (Present address: National Grassland Research Institute, Nishinasuno, Tochigi 329-27, Japan)*

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Abstract

Isolates of *Typhula ishikariensis*, a snow mold fungus, were collected from five localities in Norway. They were divided into three groups according to genetics, cultural morphology, etc. Group I grew normally at 10 °C. Its mating patterns with Japanese taxa were variable: compatible with both biotypes A and B; compatible with biotype A but incompatible with biotype B; and incompatible with both biotypes. Group I was prevalent in southern inland districts such as Buskerud, Oppland, and Hedmark. Group II had smaller sclerotia as compared to other groups, and its sclerotia were often covered with white mycelium in nature and in culture. Group II was compatible with biotype B only. Group III was characterized by irregular growth at 10 °C and genetic incompatibility with biotypes A and B. Cultural morphology of group III resembled that of group I at 0 °C. Rind cell patterns of sclerotia did not separate these two groups or biotypes. Isolates of groups II and III were often obtained from coastal regions in Finmark. Mating reactions were variable: monokaryons were compatible with their respective dikaryons, and monokaryons of groups II and III occasionally mated with group I dikaryons. Dikaryons of groups II and III, however did dikaryotize monokaryons of other groups. Norwegian isolates of *T. ishikariensis* were highly variable, and the orthodox nomenclature system seemed inapplicalbe at the infraspecific level.

Introduction

The snow mold fungus, *Typhula ishikariensis* S. Imai is widely distributed in the northern hemisphere but contrasts with other ubiquitous snow mold fungi in that this species has evolved specialized forms adapted to different winter climates (Matsumoto, 1992; 1995), constructing the *T. ishikariensis* complex. In the U.S.A., two taxa, i.e. *T. ishikariensis* and *T. idahoensis* Remsberg, were recognized as separate species (Bruehl and Cunfer, 1975; Bruehl et al., 1975). These two species were not interfertile and differed in habitat and host range. Årsvoll and Smith (1978), on the contrary, did not recognize *T. idahoensis* as a separate species since these two species were found, at least, partially interfertile and divided *T. ishikariensis* into three varieties including var *ishikariensis*, var. *idahoensis*, and var. *canadensis* var. nov. based on rind cell patterns and sporocarp size. Christen and Bruehl (1979) later found putative hybrids in nature, which mated with both of these two species, and included var. *canadensis* within the range of variation of *T. idahoensis* isolates (Bruehl and Machtmes, 1980). Matsumoto et al. (1982) identified three groups within Japanese isolates of *T. ishikariensis* and referred to them as biotypes. Biotype A mated with var. *ishikariensis* but not with other biotypes, and biotypes B and C were compatible with each other and with var. *idahoensis* and var. *canadensis* (Matsumoto et al., 1983). Biotype A, var. *ishikariensis*, and var. *idahoensis* were

indistinguishable in cultural morphology (Bruehl and Matchmes, 1980; Matsumoto et al., 1982). Biotype C, resembling var. *canadensis* in culture morphology, was considered to represent one end of a continuum of variation in biotype B isolates (Matsumoto and Tajimi, 1990) and, on genetic evidence, was referred to as the small sclerotium (ss) form of biotype B (Matsumoto and Tajimi, 1991). In addition, Ekstrand (1955) described *T. borealis* and *T. hyperborea* from Fennoscandia, but type specimens are not available. These two species differ in the shape of basidiospores, host range, growth temperature relations, and cultural morphology.

Thus, the taxonomic confusion of the *T. ishikariensis* complex has been resolved to some extent during the last two decades; however, corresponding taxa from different regions do not always exhibit the same characteristics in this highly endemic species. For example, var. *canadensis* is adapted to severe winters in Canada (Årsvoll and Smith, 1978), but the ss form of biotype B predominates in the southernmost habitat of *T. ishikariensis* in Japan where snow cover seldom occurs (Honkura et al., 1986). Russian isolates of var. *ishikariensis* attack underground parts of tulips (Sinadskii and Tkachenko 1981), but biotype A never occurs on tulips in Japan (N. Matsumoto, unpubl.).

Matsumoto and Tronsmo (1995) collected isolates of *T. ishikariensis* from Norway and tentatively classified them into three groups. Group I isolates resembled biotype A, var. *ishikariensis* and var. *idahoensis* in cultural morphology grown at 9 °C, and they showed three different mating patterns with biotypes A and B. Group II isolates were characterized by abundant aerial mycelium and exclusive compatibility with biotype B. Group III isolates were all incompatible with biotypes A and B, and cultural morphology at 9 °C was distinct from other taxa. Critical mating experiments and morphological comparisons in the present investigation suggest that isolates of *T. ishikariensis* are highly variable and that the universal infraspecies nomenclature system is not feasible in the *T. ishikariensis* complex.

Materials and methods

Fungal isolates. A total of 529 isolates of *T. ishikariensis* was obtained from 22 sampling sites in 7 communes belonging to the counties of Buskerud, Finnmark, Hedmark, and Oppland in Norway (Figure 1). The Buskerud-Oppland locality was in the east of Hardangervidda, consisting of communes of Hemsedal, Nord-Aurdal, and Øystre Slidre. The Hedmark locality included a sampling site in Åmot to the east of lake Mjøsa. The Oppland locality consisted of sampling sites in Fron located in the east of Jotunheimen. These three localities represented inland habitats with little soil freezing (Årsvoll, 1973). The two Finnmark localities consisted of sites in Alta and Sør-Varanger, representing coastal habitats with frequent soil freezing (Årsvoll, 1973).

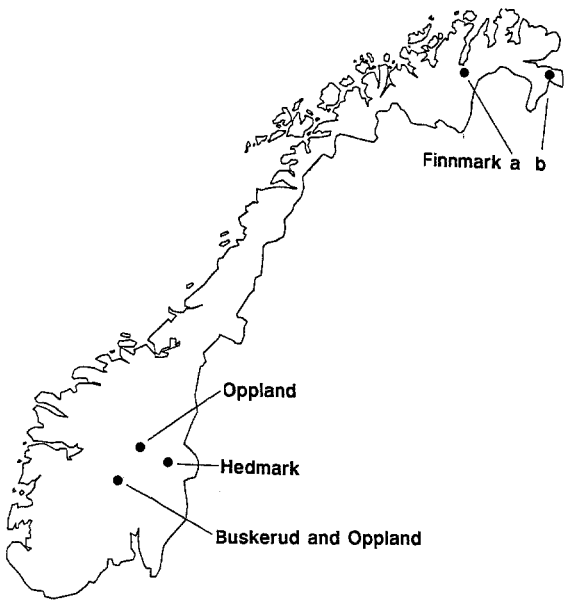

Figure 1. Localities in Norway from which *Typhula ishikariensis* isolates were collected.

All the dikaryotic isolates originated from sclerotia produced on diseased grasses. Each locality included isolates belonging to the same vegetative compatibility groups (VCG) (Matsumoto and Tronsmo, 1995). Here, each VCG was referred to as a strain, and most results were presented on the basis of strain to avoid overlapping of isolates of the same genotype. Fifty Norwegian strains were used for critical experiments, consisting of 26, 10, and 14 strains of groups I, II, and III, respectively. Two, 1, and 3 samples of groups I, II, and III developed sporocarps from natural sclerotia, respectively, and monosporous cultures (monokaryons) were obtained from each sporocarp. Cultures were maintained on potato-dextrose agar (PDA) slants at 4 °C.

Mating experiments. Mating experiments between monokaryons (mon-mon matings) and between

dikaryon and monokaryon (di-mon matings) were conducted as previously described (Matsumoto et al., 1983); 5-mm diam agar discs with mycelia were cut from the margin of actively growing PDA cultures and placed ca. 2 cm apart on PDA plates. After two weeks incubation at 4 °C (where group II isolates were involved) or at 10 °C (where group II isolates were not involved), a small agar block was cut from the junction of the colonies for mon-mon matings and from the monokaryon colony 5 mm behind the junction for di-mon matings and transferred to the unoccupied portion of the same plate. Growth from the block was examined for clamps several days later. Presence of clamps was the criterion of compatible mating. The symbol '+' shows a compatible combination with vigorous growth from the block. When the growth was normal but lacked clamps, the combination was incompatible, and the symbol '−' was given. The symbol '±' shows the combination in which the growth was poor with a few clamps on irregularly ramified hyphae, and '=' indicates poor growth with no clamps. 'L' and 'l' show lateral dikaryotization with vigorous and poor growth from the block, respectively. The latter 4 classes were regarded as incompatible. Where results were contradictory with different tester monokaryons of the same taxa, the involvement of common mating allele(s) was not ruled out and the combinations were regarded as compatible. One monokaryon each of biotypes A (PR9-4-4) and B (8-1) was used as Japanese testers in most cases.

Rind cell patterns of sclerotia. Rind cell patterns of sclerotia of mature sclerotia of Norwegian groups I and III and Japanese biotypes A and B, produced on approximately one-month-old cultures on PDA plates, were examined under the microscope. Indices of 0 to 4 were assigned according to the complexity of rind cell patterns based on the photographs of Årsvoll and Smith (1978), i.e. 0: typical of *T. ishikariensis* var. *ishikariensis* exclusively with rounded cells; 1: similar to var. *ishikariensis* with a few lobate cells in addition to many rounded cells; 2: intermediate both with a few rounded cells and with a few lobate cells; 3: similar to var. *idahoensis* mostly with lobate, interlocking cells and with a few rounded cells; and 4: typical of var. *idahoensis* mostly with lobate and noticeably interlocking cells.

Growth temperature relations and cultural morphology. Mycelial discs, 5 mm in diameter, were cut from the margins of actively growing colonies, transferred to 9 cm diameter Petri plates containing PDA and incubated in duplicate at 0 and 10 °C for up to 40 days. After 21 and 14 days' incubation at 0 and 10 °C, respectively, colony diameter was determined, and mycelial growth rate per day was calculated for each culture. Where colonies of group III strains were irregular at 10 °C, the largest diameter was measured. Then, cultures were further incubated at the same temperatures, and cultural morphology was compared at the end of incubation. PDA cultures were incubated also at 12 °C for 30 days to emphasize the differences in cultural morphology between groups I and III.

Results

Distribution of groups. One hundred and thirty-five strains from the Buskerud-Oppland locality were all group I (Table 1, Figure 1). The Hedmark locality had group III as well as group I. Groups II and III were found frequently from the Oppland locality but there were few group I isolates. In the two Finnmark localities, group III predominated, and other groups were infrequent (Table 1).

Genetic characteristics. Most group I strains were compatible with biotype A. Group II was compatible exclusively with biotype B, and group III was incompatible with both biotypes.

A complete set of four monokaryons with different mating compatibility alleles was obtained from two group I sclerotial samples (2–5BS and 3–1BS) and one group III sample (6–1AS), indicating that groups I and III were bifactorial. A group II sample (4–3S) produced three different monokaryons, and a 4th was not found. Intersample matings within group I were all compatible, but this was not the case with group III. Group II was incompatible with other groups as was group III (Table 2).

When selected monokaryons of groups I, II, and III were paired with the 50 dikaryotic strains, genetic relationships between groups became clear (Table 3). Group I was compatible with all the groups; group I dikaryons, including those incompatible with both biotypes, were effective as a nucleus donor to other groups. Groups II and III were compatible only with the same group; they were donors to their respective receptor monokaryons. Though group I strains were divided into three subgroups by the mating reactions of Japanese testers, they were not distinguished by the reactions of Norwegian testers.

Table 1. Mating reaction of tester monokaryons of biotypes A and B to Norwegian strains of *Typhula ishikariensis*[x]

Locality[y]	Number of strains designated as groups[z]				
	I			II	III
	A+B+	A+B−	A−B−	A−B+	A−B−
Buskerud and Oppland (7)	4	116	15	0	0
Hedmark (1)	0	10	4	0	7
Oppland (4)	0	1	1	15	23
Finnmark a (6)	0	7	1	7	67
Finnmark b (4)	0	0	0	1	81

[x] Figures indicate number of strains. Isolates belonging to the same VCGs were regarded as strains. VCGs between localities were not determined.
[y] Figures in parentheses indicate the number of sampling sites.
[z] A: biotype A; B: biotype B; +: compatible; −: incompatible.

Table 2. Mating patterns between monokaryons of Norwegian *Typhula ishikariensis*[x]

		2–5BS (I)				3–1BS (I)				4–3S (II)				6–1AS (III)				6–1BS (III)		
		1	3	8	2	1	6	8	5	6	9	4	5	1	8	18	2	1	16	4
2–5BS[y] (I)	1	−	−	−	+															
	3	−	−	+	−															
	8	−	+	−	−															
	2	+	−	−	−															
3–1BS (I)	1	+	+	+	+	−	−	−	+											
	6	+	+	+	+	−	−	+	−											
	8	+	+	+	+	−	+	−	−											
	5	+	+	+	+	+	−	−	−											
4–3S (II)	6	−	l	−	l	−	−	−	−	−	−	−	+							
	9	−	−	−	−	−	−	−	−	−	−	−	−							
	4	nd	nd	nd	nd	nd	nd	nd	nd	−	−	−	−							
	5	−	−	−	−	−	l	−	−	+	−	−	−							
6–1AS (III)	1	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+			
	8	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−			
	18	−	=	l	−	−	−	−	−	−	−	−	−	−	+	−	−			
	2	−	=	−	−	−	−	−	−	−	−	−	−	+	−	−	−			
6–1BS (III)	1	−	−	−	−	−	−	−	−	−	−	nd	−	+	−	L	−	−	−	+
	16	−	=	−	l	−	−	−	−	−	−	nd	−	−	−	−	−	−	−	−
	4	−	±	−	−	−	−	−	−	−	−	nd	−	nd	nd	nd	nd	+	−	−
6–4S (III)	20	−	−	−	−	−	−	−	−	−	−	nd	−	L	L	±	l	nd	nd	nd

[x] +: compatible with vigorous growth; ±: dikaryotized with poor growth, L: unilateral dikaryotization, dikaryotized hyphae grew vigorously; l: unilateral dikaryotization, dikaryotized hyphae grew poorly with a few clamps; and −: incompatible with vigorous growth. nd: not determined.
[y] Figures in parentheses indicate groups.

Rind cell patterns. Each taxon showed a variety of rind cell patterns (Figure 2). Norwegian group I could not be distinguished from group III by rind cell patterns, and this was the case with Japanese biotypes even though biotype A tended to have more rounded cells (Table 4). VCGs 3–1A, 4–3, and 4–5 represented 3 different strains, consisting of 16, 10, and 15 group III isolates, respectively. Fifteen isolates belonging to VCG 4–5 had lobate, var. *idahoensis* type of rind cells with little isolate variability; however VCGs 3–1A and

Table 3. Mating reactions between Norwegian isolates of *Typhula ishikariensis*[x]

	Reactions of tester monokaryons of groups[y]								
	I			II			III		
	+	±	−	+	±	−	+	±	−
Dikaryons of group I[z]									
(A+B+)	14	2	0	3	1	6	9	16	5
(A+B−)	32	2	2	6	1	13	30	25	5
(A−B−)	16	4	8	5	3	12	33	22	5
	(77.5)			(28.0)			(48.0)		
group II	0	0	20	19	0	1	0	0	60
	(0.0)			(95.0)			(0.0)		
group III	0	0	28	0	0	28	66	7	11
	(0.0)			(0.0)			(78.6)		

[x] Twenty-six, 10, and 14 strains (dikaryons) were paired with 2 or 4, 2, and 6 monokaryons of groups I, II, and III, respectively. Figures indicate the number of combinations. Figures in parentheses indicate the percentage of compatible combinations.

[y] +: compatible, hyphae dikaryotized with vigorous growth; ±: incompatible, hyphae with a few clamps and poor growth; and -: incompatible, hyphae not dikaryotized with vigorous growth.

[z] A+B+: compatible both with biotypes A and B; A+B−: compatible with biotype A, incompatible with biotype B; and A−B−: incompatible with both biotypes.

Table 4. Rind cell patterns of sclerotia of *Typhula ishikariensis* isolates from Norway and from Japan[x]

	Rind cell patterns[y]			
	0	1	2	3
Taxon				
group I	17	75	94	32
group III	12	63	70	69
biotype A	10	12	7	3
biotype B	4	16	9	18
VCG[z]				
3–1A	0	8	3	5
4–3	1	3	3	3
4–5	0	0	8	7

[x] Figures indicate number of isolates.

[y] 0: typical of var. *ishikariensis* exclusively with rounded cells; 1: similar to var. *ishikariensis* with a few lobate cells in addition to many rounded cells; 2: intermediate both with a few rounded cells and with a few lobate cells; and 3: similar to but not typical of var. *idahoensis* mostly with lobate cells and with a few rounded cells.

[z] Vegetative compatibility groups each designating locality of samples. Sixteen, 10, and 15 group III isolates from each locality were of the same VCGs.

Table 5. Mycelial growth rate of Norwegian *Typhula ishikariensis*

Group[x]	Incubated at		Relative growth[z]
	0 °C[y]	10 °C[y]	
I	1.26 ± 0.12a	2.11 ± 0.21a	60.4 ± 6.77a
II	0.98 ± 0.14b	1.68 ± 0.22b	58.6 ± 9.06a
III	1.00 ± 0.09b	1.39 ± 0.19c	72.7 ± 8.37b
F	30.29***	54.79***	14.17***

[x] Twenty-six, 10, and 14 strains each of groups I, II, and III were used, respectively.

[y] PDA cultures were grown for 21 and 14 days at 0 and 10 °C, respectively in duplicate. Figures indicate growth rate (mm/day) ± standard deviation.

[z] Relative growth at 0 °C to 10 °C. Figures indicate % ± standard deviation. Figures with the same alfabet are not significanltly different at the 5% level within each colum according to Tukey's multiple range test.

***: significant at the $p < 0.001$ level.

4–3 exhibited considerable variability (Table 4). There was no isolate with sclerotial rinds with lobate, noticeably interlocking cells classified as 4.

Growth temperature. Group I strains grew fastest at both 0 and 10 °C. The mycelial growth rates of groups I and II were reduced to about 60% at 0 °C (Table 5). Group III strains grew most slowly at 10 °C, but growth rates were almost similar to other groups at 0 °C.

Cultural morphology. At 0 °C, some group III stains had fluffy aerial mycelium, but others were indistinguishable in cultural morphology from group I strains (Figure 3). However, at 10 °C, their hyphae became gnarled and irregularly branched, making mycelium appressed and feather-like (Figure 3). At this temperature a few sclerotia coalesced to form large, irregular sclerotia often with exudates on them (Figure 3). Such differences were more pronouced at 12 °C; four group III strains grew as poorly as at 10 °C, and 10 became much deteriorated. All the group I strains compatible with Japanese biotype(s) grew well at 12 °C except one. Of 9 group I strains, which were incompatible with Japanese biotypes, 4 had reduced growth with irregular colony margin, making intergrades with group III (Figure 4).

Group II isolates from the Oppland locality often had abundant aerial mycelium, consisting of strongly ramified hyphae. Their sclerotia were small and covered with thick mycelium. Those sclerotia developed normal sporocarps and produced basidiospores.

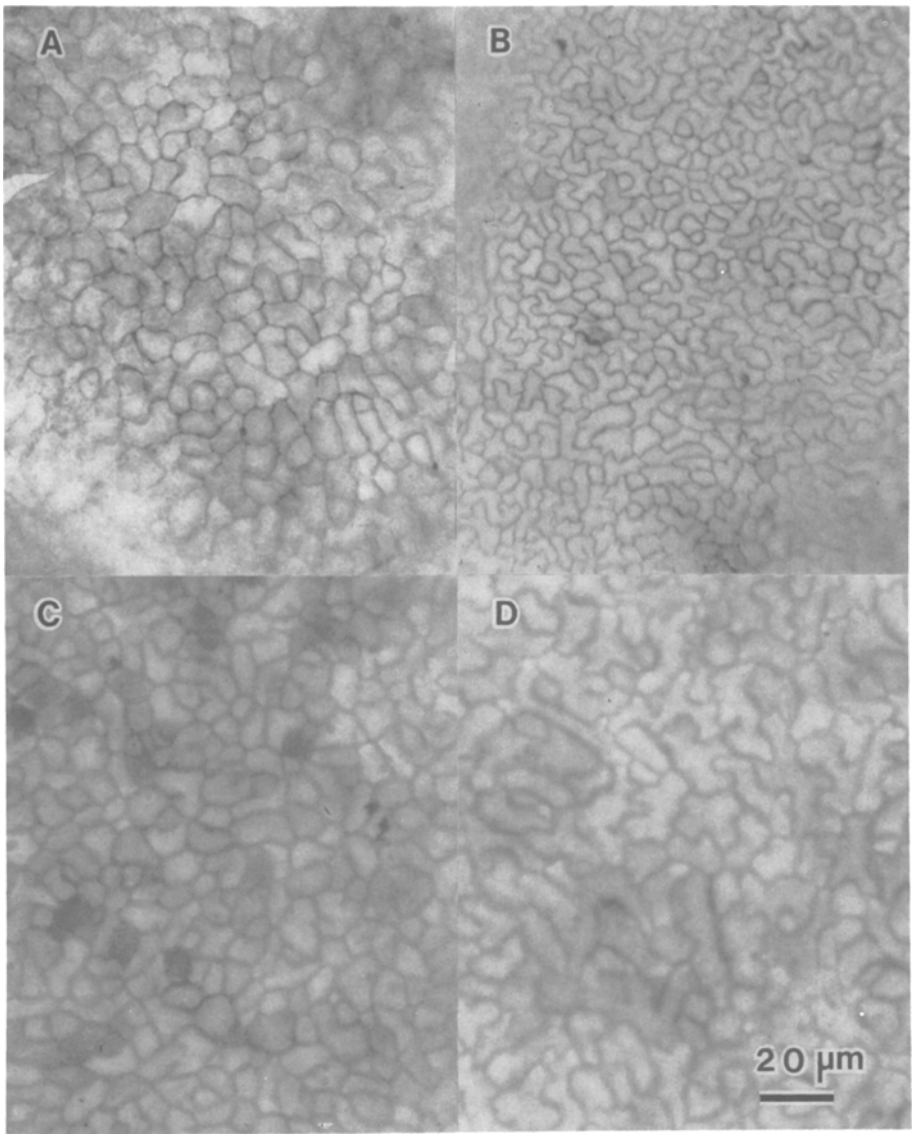

Figure 2. Rind cell patterns of mature sclerotia. (A) and (B) group III isolates with rounded (rated as 0) and lobate cells (rated as 3), respectively. (C) and (D) biotype A isolates with rounded and lobate cells, respectively.

Surface mycelia covering sclerotia tended to disappear after subsequent transfers.

Discussion

Årsvoll and Smith (1978) regarded *T. ishikariensis* var. *canadensis* as synonymous with *T. hyperborea* and with some intermediate forms within the *T. ishikariensis* complex due to their adaptation to lower temperatures and some other ecological traits though they were unable to compare *T. borealis* and *T. hyperborea* with *T. ishikariensis* because of the lack of type specimens. Var. *canadensis* resembles some group II isolates with abundant aerial mycelium and small sclerotia. Consequently, groups II could be considered synonymous with *T. hyperbores*. However, they do not seem to represent the same taxon; basidiospores of a group II sample were sub-cylindrical to oblong-ovate but not ovate. Ekstrand (1955) distinguished *T. hyperborea*

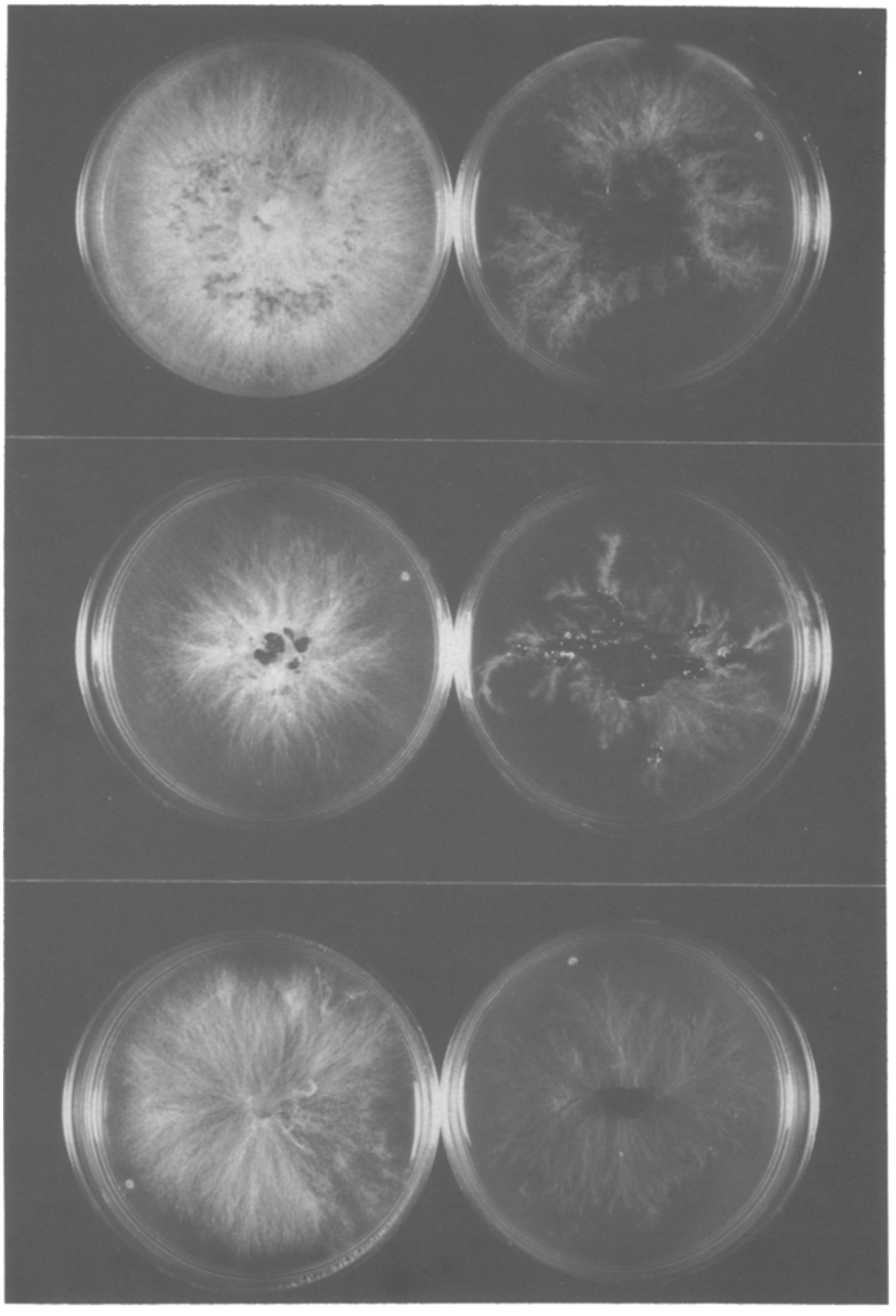

Figure 3. Macromorphology of 40-day-old PDA cultures of group III strains. Three strains in pairs. Left column grown at 0 °C, and right at 10 °C.

by its ovate basidiospores, but var. *canadensis*, as well as var. *ishikariensis* and var. *idahoensis*, does not have ovate basidiospores (Årsvoll and Smith, 1978). Though we failed to observe basidiospores of group III, *T. hyperborea* is more likely to be identical to group III due to its adaptation to low temperatures (or poor growth at higher temperatures). The spore shape and host range of group III should be investigated to reveal the identity of these two taxa.

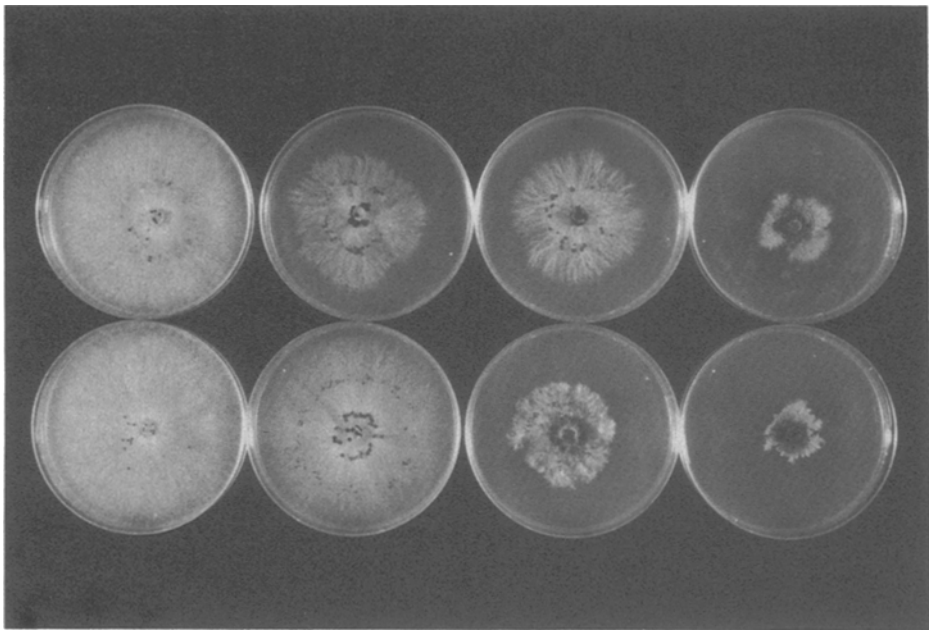

Figure 4. Continuous variation in cultural morphology grown at 12 °C within strains of groups I and III. Left 4: group I strains and right 4: group III strains.

We consider that groups I and III correspond to *T. borealis* and *T. hyperborea*, respectively. There was, however, no clear demarcation between these two groups, which included a wide range of variation in cultural morphology and mating patterns with Japanese biotypes. Several strains, which were incompatible with biotypes A and B, were included in group I because of the normal growth at 10 °C; and group III strains were invariably incompatible with Japanese taxa but variable in cultural morphology. They may be regarded as a single taxon. Group III seems to represent a group of strains which are adapted to colder temperatures especially in coastal regions. There, plants are often killed due to freezing (Årsvoll, 1973). Sclerotia of group III from field materials were indistinguishable from those of group I since they had been produced at 0 °C or below it. Rind cell patterns of sclerotia cannot be the criterion either since they were not associated with group or biotype designation. We do not know if rind cell patterns are affected by environmental conditions.

Group II was more uniform than other groups. Group II strains were similar in cultural morphology and genetics to the ss form of biotype B and to var. *canadensis*. Their mycelia produced on infected plants were usually, but not always, very fluffy. Their sclerotia were often covered with white mycelium, leading us to consider that they had been colonized by a mycoparasite under snow. The sclerotia were, however, all viable, and no other fungus was isolated from them. Smith (J. D. Smith, pers. comm.) considered this character of sclerotia as an adaptation to wind dissemination. Var. *canadensis* leaves fluffy mycelium on infected plants (Smith, 1987), but this is not the case with the ss form of biotype B (N. Matsumoto, unpub.).

So far as the Norwegian and Japanese taxa are concerned, the *T. ishikariensis* complex consists of two major subgroups which are genetically separate to different extents. One consists of groups I and III and biotype A. The two Norwegian taxa include a wide range of continuous variation in cultural morphology and in genetics associated with different winter climates, and the Japanese taxon shows little variation adapted to a very snowy habitat. The other is group II and biotype B. The Norwegian taxon, group II, is not very variable, but the Japanese taxon, biotype B, exhibits a range of variation.

Infraspecific differentiation appears to occur very locally in the *Typhula ishikariensis* complex since this fungus is highly endemic and restricted to snowy regions. Corresponding taxa between Norway and Japan were too variable to be referred to as universal

taxa such as varieties. The range of variation of *T. ishikariensis* isolates needs to be examined before infraspecific appellations are assigned.

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