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Allopatry of the Pathogenic Species of *Typhula*, Snow Mold Fungi: Its Ecological Implications

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Abstract

There are two pathogenic species of *Typhula* which cause snow mold in Japan, i.e. *T. incarnata* and *T. ishikariensis*. *T. ishikariensis* includes biotypes A and B, and isolates of biotype B show continuous variation associated with climatic conditions in winter. The distribution patterns of these fungi are allopatric. *T. incarnate* is ubiquitous with versatility in various ecological characteristics. *Typhula ishikariensis* biotype A distributes in snowy areas. Although its aggressiveness is intermediate, its strong competitive ability for less hardened plants enables the fungus to prevail in snowy areas, monopolizing the best resources for the pathogens. Biotype B exists mainly in less-snowy areas, where the host plants are rather hardy. However, strong aggressiveness of biotype B allows the fungus to attack those resources without waiting for the deterioration of the host plants under snow cover conditions. It is concluded that *T. Incarnata* has a general adaptability, while *T. ishikariensis* has a specific adaptability to varying environments.

Discipline: Plant diseases
Additional key words: allopatric distribution, *Typhula incarnate, Typhula ishikariensis*

Introduction

Fungi of several taxonomic groups can grow under drifted snow, infect selected host plants, and cause considerable damage to them, which are called snow mold. Some of the best known fungi are pathogenic *Typhula* spp. (Basidiomycotina). They are generally obligate snow mold, the existence of which is closely associated with persistent snow cover. A general model of their life cycle is schematically shown in Fig. 1. The pathogenic species of *Typhula* are active during the winter season, when their hosts are dormant, while they pass through a resting stage during the summer season. Sclerotium is the resting structure of the majority of *Typhula* spp., and it enables those fungi to survive the desiccation and high temperature environments during the period of spring to autumn, the growing season of their host plants. The sclerotium germinates carpogenically and/or myceliogenically in late autumn. Plant tissues are infected by mycelium and/or basidiospores. The disease advances through the winter months, during which period numerous sclerotia are produced on host plants before thawing of snow cover in early spring.

The pathogenic species of *Typhula* are essentially opportunistic parasites which attack their host plants under snow cover as their resistance is lowered due to impaired photosynthesis and resulting exhaustion of reserve materials. Another significant role played by snow cover is that it constantly maintains low temperature, which reduces microbial antagonism⁹⁾. The optimum temperature for growth of the pathogenic species of *Typhula* in axenic culture is about 7–12°C. However, when the cultures are covered with unsterile soil to introduce antagonism from other microorganisms and incubated at 10°C, mycelial growth is almost completely suppressed. However, at 0°C, i.e. the ambient temperature under snow cover, they grow as vigourously on the plates covered with soil as in axenic culture and attain about half of their maximal growth capacity (Plate 1).

In Japan, there are two *Typhula* species causing snow mold, i.e. *T. incarnata* Lasch. Fr. and *T. ishikariensis* S. Imai, among which three biotypes are recognized[11]. Physical conditions under snow cover are characterized by low temperature and high humidity, which are both essential to the obligate snow mold fungi as described earlier. During the winter season in Japan, these physical conditions do not greatly vary from place to place but remain rather constant, while the duration of persistent snow cover varies considerably. It is very likely that this parameter is the most relevant factor in causing their allopatric distribution. It is observed that each fungus having its own life-history shows a specific distribution pattern, which seems to be primarily determined by snow cover conditions, i.e. duration of the persistent snow cover and stability in its annual fluctuation. This paper attempts to discuss allopatric distributions of the pathogenic species of *Typhula* in Japan, with special reference to their evolutionary biology, so that the mode of their niche separation could be identified.

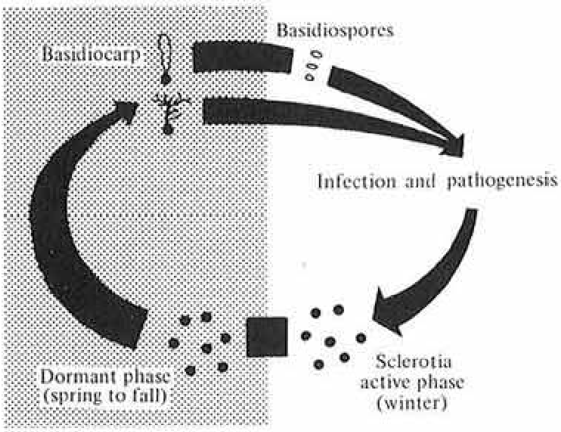

Fig. 1. Life cycle of the pathogenic species of *Typhula*

Pathogenic species of *Typhula*

Typhula incarnata and the *T. ishikariensis* complex are the major plant pathogens of the genus *Typhula*. There is no taxonomic dissent on *T. incarnata,* but there is still controversy concerning the taxonomy of the members of the *T. ishikariensis* complex. In the United States, the complex includes *T. ishikariensis* and *T. idahoensis* Remsberg[4], and in Canada, *T. ishikariensis* var. *ishikariensis,* var. *idahoensis,* and var. *canadensis*[3]. Matsumoto et al.[11] identified three groups in Japanese isolates of *T. ishikariensis,* referring to them as biotypes A, B, and C. Some of these members are synonymous. Biotype A, being identical to *T. ishikariensis* in USA as well as var. *isikariensis* in Canada, has brown sclerotia and produces sparse to moderate aerial mycelium on potato-dextrose agar. Biotype B is characterized by dark brown to black sclerotia and produces moderate to abundant aerial mycelium. It does not resemble any other taxa in culture morphology. Biotype C and var. *canadensis* both produce minute sclerotia and are indistinguishable

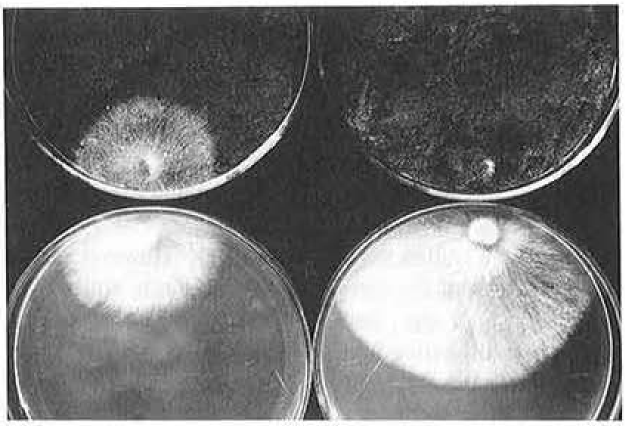

Plate 1. Mycelial growth on potato-dextrose agar with (top row) and without (bottom row) soil cover at 0°C (left row) and 10°C (right row)

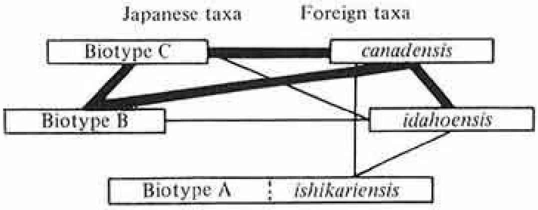

Fig. 2. Genetic relationships within the *Typhula ishikariensis* complex
Two taxa tied by a heavy line or by a fine line are closely or slightly related, respectively. Untied taxa are not related with each other.

on cultural characteristics.

Genetic relationships within the *T. ishikariensis* complex are shown in Fig. 2[12]. The taxa connected by thick and fine lines are related closely and distantly, respectively, and in case where there is no connecting line, those taxa are not genetically related. In Japan, biotype A is separate from other biotypes, but it was confirmed that it shares common mating incompatibility alleles with American *T. ishikariensis*. Biotypes B and C are closely related, and both can mate with *T. idahoensis* and *T. ishikariensis* var. *canadensis*. In fact, these biotypes have recently been found to form a single taxon as described later. In North America, all the taxa can mate each other, indicating their close relationships.

Biotype A is moderately aggressive and can attack both di- and monocots. Biotypes B and C are most aggressive and prevail on monocots only. *Typhula incarnata* is least aggressive but capable of saprophytic growth, which *T. ishikariensis* does not show[7].

Allopatric distribution in Japan

Complex geographic conditions in northern Japan contribute to the diversity in the winter climate of this region in general, and the duration of snow cover in particular. The allopatry of the pathogenic species of *Typhula* is greatly influenced by those snow cover conditions and, to a lesser extent, by interactions between the existing taxa[8].

Biotype A of *T. ishikariensis* is observed exclusively in the areas where snow cover of 50 cm deep lasts for, at least, 60 days a year (referred to as the biotype A area). Biotype B is distributed mainly in the areas of less snow, where biotype A does not exist (the biotype B area). *Typhula incarnata* is widely distributed, being more abundant in the biotype A area. Both biotypes, however, coexist in the intermediate areas by colonizing different host species: biotype A grows on plant species such as winter cereals and ryegrasses which are less winter hardy and more susceptible to the attack of *Typhula*, while biotype B grows on winter hardy plant species such as orchardgrass, fescues, and weeds of the Cyperaceae and Junaceae. *Typhula incarnata* can thrive on senescent and moribund tissues which *T. ishikariensis* can not colonize.

The optimal habitat for the pathogenic species of *Typhula* is the biotype A area, since the plants growing there tend to be more susceptible to the disease attack than those in the biotype B area[2]. It is also likely that the cloudy and rainy weather conditions in autumn of the biotype A area[6] affect host resistance since sunshine generally increases the level of winter hardiness of plants[1]. In addition, snow cover in the biotype A area occurs invariably each year and persists for a long period of time. A possible reason why biotype B possessing strong aggressiveness does not prevail in the biotype A area was identified from the inoculation experiment, which indicated that biotype A excluded biotype B and *T. incarnata*. In the biotype B area, the snow cover does not last long, and plants are more resistant to diseases due to more abundant sunshine in autumn. Strong aggressiveness of biotype B may enable it to attack such plants before their resistance has been lowered under senescence or adverse conditions.

Fig. 3 diagrammatically presents niche separation in the pathogenic species of *Typhula*. The best resources that are nutrient-rich, easy to exploit, and not already colonized by other microorganisms, are monopolized by biotype A, since this fungus is most competitive on such resources. Because of its strong aggressiveness, biotype B can infect the hardy plants which are highly resistant and nutrient-rich. The saprophytic ability of *T. incarnata* is utilized in the colonization of weathered, nutrient-depleted substrates on which other microorganisms have already become established. Biotype C behaves the same way as biotype B does, although it has been difficult until recently to define its niche because of its indefinite distribution and limited information available.

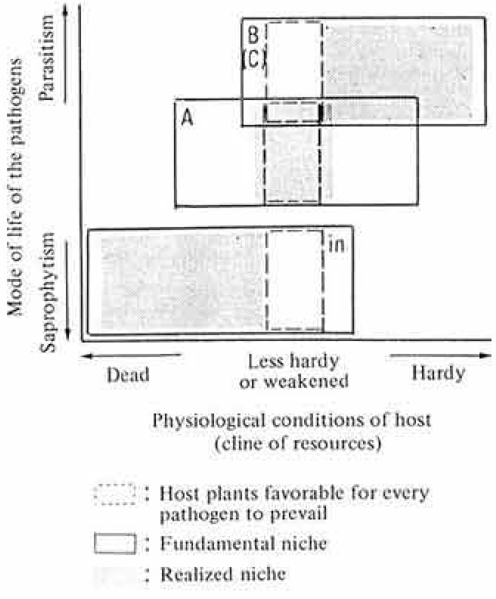

Fig. 3. Diagrammatic presentation of niche separation of *Typhula incarnata* (in) and *T. ishikariensis* biotypes A (A), B (B) and C (C)

Fig. 4. Localities of isolates of *Typhula ishikariensis* biotypes B and C and the related in northern Japan

Continuous variation within isolates of *T. ishikariensis* biotypes B and C

In spring 1984, after unusually cold and snowy winter, the outbreak of *T. ishikariensis* biotype C occurred on winter cereals, such as winter barley and winter wheat, in the Sendai plain of the southern Tohoku district (Fig. 4). This incidence provided a clue to characterize the ecological nature of biotype C. In this area, snow cover of more than 20 cm deep seldom occurs and normally thaws within a week after it falls. After an extensive survey by Honkura et al.$^{5)}$, it is concluded that biotype C is endemic in the Sendai plain, and that, in normal years, it can barely survive mainly by colonizing rice stubbles. Since an intermediate, bridging group with sclerotia of intermediate size and capable of mating with both biotypes, was recognized to exist very often in Honshu, it was included within a range of variation of biotype B$^{10)}$. A large sclerotium form of biotype B occurs in Hamatonbetsu, northern Hokkaido, where snow cover conditions are most favorable in the distribution range of biotype B. The existence of two additional forms in biotype B and the close genetic relationship observed between biotypes B and C, suggest that they constitute a continuum with an identical genetic background, leading to further development of the above-mentioned hypothesis on adaptations to different snow cover conditions.

Matsumoto and Tajimi$^{10)}$ ascribed this supposed continuum to different winter climatic conditions. They collected isolates from several localities, which differ in snow cover conditions. Their investigations included sclerotium diameter and level of aggressiveness of each population to demonstrate the continuous variation within these isolates (Fig. 4 & Table 1). Sclerotium diameter differed greatly between the populations and became smaller with decreasing snow cover index (number of days with snow cover per annum/CV). No significant correlation was observed between snow cover conditions and the aggressiveness, while all the isolates from the Sendai region with an inconsistent snow cover were highly aggressive. The extent of sexuality as revealed by carpogenic germination of sclerotia (production of sexual stage) decreased with decreasing snow cover index, and the Sendai population was least sexual.

Table 1. Snow cover conditions in the 7 localities of the isolates of *T. ishikariensis* biotypes B and C, the related forms and their mean aggressiveness

Locality	Snow cover conditions			No. of isolates belonging to each formb)				Mean aggressivenessc)
	Indexa)	Mean no. of days with snow cover per annum	CV (%)	LSF	B	INT	C	
Hamatonbetsu	17.2	146.1	8.5	2	7			4.25 c
Yakumo	17.1	117.8	6.9		6	2	1	4.99 b
Abashiri	13.0	120.5	9.3		9			4.60 bc
Sapporo	12.0	122.2	10.2		5	4		4.21 c
Oomagari	6.4	119.6	18.7		1	6	2	4.56 bc
Morioka	4.7	95.7	20.6		4	5		4.56 bc
Sendai	1.2	41.5	34.0			1	8	5.53 a

a): Index: No. of days with snow cover per annum/CV.

b): Nine isolates randomly selected were used as representatives of each locality.
LSF; Large sclerotium form of biotype B having sclerotia with a mean diam. >1.25 mm, B; Biotype B with sclerotia of 0.75–1.25 mm, INT; Intermediate form with sclerotia of 0.5–0.75 mm, and C; Biotype C with sclerotia < of 0.5 mm.

c): Aggressiveness of each isolate was determined on the basis of regrowth of inoculated orchardgrass plants from 0 (no damage) to 6 (killed). The values followed by the same letter are not significantly different ($p = 0.05$) based on the Duncan's multiple range test.

In the northernmost area such as Hamatonbetsu, snow cover is constantly maintained for a long period of time, the duration of which is quite uniform year after year. Such a habitat with a high snow cover index is, therefore, constant and stable. The comparatively large sclerotia of isolates from snowy localities may have probably developed because of the stable, long winter climate, during which period reserve materials continue to accumulate. Such nutrient-rich sclerotia support the greater production of sexual stage, which results in considerable genetic variability, while the highly favorable habitat leads to decreased overall aggressiveness of the population.

The Sendai plain represents the front of the domain of the continuum, and no other pathogenic *Typhula* has been observed in this area. The environmental characteristics of the Sendai plain define the features of habitat of biotype C. In Sendai, the duration of snow cover is 41.5 days per annum. This figure, however, does not refer to a continuous snow fall but the total number of days when the ground is covered with snow. In this area, snow usually thaws within a week after it falls. This implies that biotype C can survive in soil and infect underground parts of its host plants5). Since snow cover in this area is very irregular and thaws soon, the favorable environmental conditions are ephemeral and unstable. Biotype C completes its life cycle in the soil, where temperature and moisture are relatively constant. Once environmental conditions become favorable for germination, biotype C sclerotia may produce mycelia but not basidiocarps. The strong aggressiveness of biotype C enables it to attack plants even before their resistance has been reduced during the winter season, and it produces small sclerotia which quickly mature without external stimuli in readiness for forthcoming unfavorable conditions9). The loss of the sexual stage shortens the life cycle considerably. Examples of the shortened life cycles similar to *Typhula* are reported in the short-cycled rusts of the Canadian arctic13) and in the predominance of sterile fungi of tundra soil14). Genetic identity of biotypes B and C has recently been confirmed (Matsumoto, unpublished). It is proposed that biotype C should be referred to as the small-sclerotium form of biotype B, since biotype C can be distinguished as an ecotype specialized in the unstable habitat with ephemeral snow cover.

Conclusion

Typhula incarnata and *T. ishikariensis* are obligate snow mold: the existence of which is largely dependent on persistent snow cover. These pathogenic species of *Typhula* are distributed throughout northern Japan. Each fungus has its own habitat according to snow cover conditions, i.e. the duration of persistent snow cover and annual fluctuation; to its adaptability of ecological characteristics and, to a lesser extent, to competitive interactions among those fungi. The versatility of *T. incarnata* in various ecological characteristics enables this species to survive in diverse habitats: this fungus can thus survive as a saprophyte as well, and prevail not only on plant tops but also on underground parts. It is concluded that *T. incarnata* has a general adaptability, while *T. ishikariensis* has a specific adaptability to varying habitats with different snow cover conditions. In a snowy habitat, the population of *T. isikariensis* is relatively sexual and moderately aggressive, generally attacking plant tops. Less snowy, harsh habitat restricts the survival of this fungal population, and its adapted form is practically asexual, highly aggressive and capable of attacking underground plant parts. The variation of forms within this population is rather small.

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