Incompatibility Alleles of Typhula incarnata

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ABSTRACT

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Most collections of *Typhula incarnata,* a tetrapolar species, produced viable basidiospores and vigorous monokaryons. Thirty-nine alleles of both the A and B loci were found in a sample of 32 field dikaryons. The multiplicity of incompatibility alleles precludes any information as to geographic races or of interbreeding within the species. We suspect that the sexual stage functions with frequency.

Typhula incarnata Lasch ex Fr., a snow mold fungus, is important on winter wheat (*Triticum aestivum* L.) in Washington primarily where environmental factors for snow mold are marginal (4). Under conditions more favorable to snow mold it competes poorly with *T. idahoensis* or with *Fusarium nivale*. Nevertheless, *T. incarnata* is a major pathogen because it occurs over a wider area than the more virulent *Typhula* spp. We are engaged in a study of the sexual states of the pathogenic *Typhula* spp. of Washington, including studies of the alleles of the A and B loci.

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MATERIALS AND METHODS

Sporophores were formed by sclerotia incubated outdoors in the fall. Mature sporophores were taped to petri dish lids. After 12 hr at 10 C in darkness, agar blocks of the Difco cornmeal agar (CMA) onto which the spores had fallen were shaken in 3 ml of sterile tap water to dislodge them. The spore suspension was poured serially over the surface of three dishes containing CMA and the surplus liquid was discarded. The inoculated dishes were incubated 2-3 days at 10 C at which time the germlings were transferred for further incubation.

Monokaryons from a given dikaryon were mated and the four mating classes were identified on the basis of clamp connections in compatible pairings. Vigorous

TABLE 1. Incompatibility alleles of the A and B loci in *Typhula incarnata*

Field dikaryons		Alleles of	
Culture	Origin	A	B
66-9(K)	Grant County, Washington, wheat	1, 2	1, 2
112	Caribou County, Idaho, grass	1, 10	10, 11
75-96-5	Okanogan County, Washington, wheat	1, 13	13, 21
25	Hokkaido, Japan	2, 18	14, 15
722	Finland	2, 19	16, 17
75-76-1	Douglas County, Washington, wheat	2, 39	22, 23
6313(L)	Douglas County, Washington, wheat	3, 4	3, 4
309	Valley County, Idaho, grass	3, 24	16, 19
66-5(M)	Lincoln County, Washington, wheat	5, 6	5, 6
1969-4	Spokane County, Washington, wheat	6, 7	3, 7
308	Valley County, Idaho, grass	6, 15	4, 6
2	Idaho County, Idaho, grass	8, 9	8, 9
75-24-1	Fremont County, Idaho, grass	10, 13	24, 25
306	Valley County, Idaho, grass	11, 12	3, 4
307	Valley County, Idaho, grass	13, 14	4, 12
75-99-1	Okanogan County, Washington, grass	13, 30	26, 27
6315	Okanogan County, Washington, wheat	16, 17	4, 13

(Continued)

TABLE 1. (continued)

	Field dikaryons	Alleles of	
Culture	Origin	A	B
75-52-4	Kittitas County, Washington, grass	18, 24	14, 28
75-15-1	Oneida County, Idaho, grass	18, 30	4, 29
3	Idaho County, Idaho, grass	20, 21	3, 18
75-37-2	Idaho County, Idaho, grass	20, 34	30, 31
73-4-1	Valley County, Idaho, grass	22, 23	16, 19
75-51-6	King County, Washington, grass	24, 35	16, 32
75-52-1	Kittitas County, Washington, grass	24, 36	5, 33
402	Adams County, Idaho, grass	25, 26	16, 20
75-11-2	Cassia County, Idaho, grass	27[a]	20
75-11-4	Cassia County, Idaho, grass	28, 29	6, 16
75-56-1	Pierce County, Washington, grass	29, 30	16, 34
75-57-4	Pierce County, Washington, grass	30, 33	35, 36
75-96-4	Okanogan County, Washington, wheat	30, 39[b]	37, 38
75-15-7	Oneida County, Idaho, grass	31, 32	3, 5
75-52-3	Kittitas County, Washington, grass	37, 38	5, 39[b]

[a]A complete set of testers was not obtained, so only 1A and 1B allele of this dikaryon were identified.
[b]With no duplications, 63 alleles of the A and B locus would have been found.

testers of each mating class were established on Difco potato-dextrose agar (PDA) until needed for matings with monokaryons of other dikaryons. The A and B loci were arbitrarily assigned (1). The methods used are routine and they have been presented in greater detail previously (1, 2).

RESULTS AND DISCUSSION

Thirty-nine alleles of the A and 39 of the B locus were identified within 32 field dikaryons (Table 1). In a similar study of *T. idahoensis,* 12 alleles of the A and 12 of the B locus were identified within 36 field dikaryons (2). Evidence to date indicates that A and B alleles in *Typhula* spp. are equally numerous.

We made no attempts to estimate mathematically the theoretical number of *T. incarnata* incompatibility alleles in the world (6, pages 106-109) because we have little faith in such calculations. We worked with cultures from Idaho and Washington plus one each from Japan and Finland and found 39 alleles of each locus. If the same multitude of alleles of the A and B loci (Table 2) extends over a wider geographic area, the total number could be very high. *Typhula incarnata* is yet another holobasidiomycete for which the question can be asked, why are there so many incompatibility alleles? On a mathematical basis such numbers seem to be unnecessary to facilitate out-crossing (6, page 244). Is inbreeding in this species so harmful that it warrants this abundance of incompatibility alleles?

The geographic distribution of duplicated alleles (Table 3) provides no evidence of recent interbreeding. For example, A2 was found in Washington, Japan, and Finland and B16 was found in Finland and in widely separated localities in Washington and Idaho, the latter 800 km apart. Perhaps some alleles form more frequently than others, and this, rather than interbreeding, accounts for their increased frequency.

Typhula incarnata was fertile throughout Washington and Idaho. In contrast, *T. idahoensis* from Idaho and adjacent Utah was almost sterile (2). *Typhula incarnata* is less virulent than *T. idahoensis* on winter wheat, but it is more widely distributed. Outbreeding would increase variability and reduce fitness to a specific environment, but this variability could permit survival over a wider

TABLE 2. Duplication of alleles of the A and B incompatibility loci in 32 dikaryons of *Typhula incarnata*

Degree of duplication	Alleles of locus	
	A	B
None, found only once	27	30
× 2	5	4
× 3	3	1
× 4	3	1
× 5	1	1
× 6	0	1
× 7	0	1

TABLE 3. Geographic distribution of frequently duplicated alleles of incompatibility loci A and B of *Typhula incarnata*

Alleles	Distribution
A2	Douglas and Grant Counties, Washington; Finland, Japan
A13	Okanogan County, Washington; Fremont and Valley Counties, Idaho
A24	King and Kittitas Counties, Washington; Valley County, Idaho
A30	Okanogan and Pierce Counties, Washington; Oneida County, Idaho
B3	Douglas and Spokane Counties, Washington; Idaho, Oneida and Valley Counties, Idaho
B4	Douglas and Okanogan Counties, Washington; Oneida and Valley Counties, Idaho
B5	Lincoln and Kittitas Counties, Washington; Oneida County, Idaho
B16	King and Pierce Counties, Washington; Adams, Cassia, and Valley Counties, Idaho; Finland

range of conditions (5). The high fertility of *T. incarnata* leads us to conclude that this species utilizes its sexual stage frequently.

We present our results as if the alleles of the incompatibility loci as designated function perfectly in all combinations. This is not true. In a few cases mating occurs where it is not expected, or does not occur where it "should". We believe that the incompatibility "loci" are in reality very complex and that alleles designated A1, for example, are not identical, but only sufficiently alike to recognize each other in most matings. If a continuum in degrees of likeness exists, some "mistakes" in recognition should be expected. Christen (3, Table 1) reports such inconsistencies in *Typhula ishikariensis*.

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