APPLIED AND ENVIRONMENTAL MICROBIOLOGY, Feb. 1994, p. 454–458
0099-2240/94/$04.00+0

Vol. 60, No. 2

Ecology of Thermophilic Fungi in Mushroom Compost, with Emphasis on *Scytalidium thermophilum* and Growth Stimulation of *Agaricus bisporus* Mycelium

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Received 20 September 1993/Accepted 11 November 1993

Twenty-two species of thermophilic fungi were isolated from mushroom compost. *Scytalidium thermophilum* was present in the compost ingredients, fresh straw, horse droppings, and drainage from compost and dominated the fungal biota of compost after preparation. Of 34 species of thermophilic fungi tested, 9 promoted mycelial growth of *Agaricus bisporus* on sterilized compost: *Chaetomium thermophilum*, an unidentified *Chaetomium* sp., *Malbranchea sulfurea*, *Myriococcum thermophilum*, *S. thermophilum*, *Stilbella thermophila*, *Thielavia terrestris*, and two unidentified basidiomycetes. These species will be considered for future experiments on inoculation and more controlled preparation of compost.

The white button mushroom, *Agaricus bisporus*, is cultivated on mushroom compost, a composted mixture of wheat straw, horse manure, chicken manure, and gypsum. Compost is prepared in a sequence of processes. After mixing and moistening of ingredients, the mixture is left for a short period to start self-heating. Then phase I is implemented; this consists of uncontrolled self-heating for 6 days in windrows in the open air. It is followed by phase II, controlled aerobic composting at 45°C for 6 days (18).

During preparation, microorganisms degrade about 40% of the dry matter of compost, the dry matter being of potential value for the nutrition of *A. bisporus*. However, only phase II compost, not the ingredient mixture nor phase I compost, is a selective substrate for *A. bisporus* (18). Thermophilic microorganisms in compost have been studied extensively (16). It remained difficult to state the dominating species among actinomycetes, other bacteria, and fungi. Using data of Sparling et al. (31), we estimated the biomass ratio of fungi to prokaryotes in compost after phase II to be 1.8:1. Wiegant (41) found ratios of 0.9:1 and 2.3:1 for conventional and experimental composts, respectively. Clearly fungi were abundant; this was also observed microscopically (1, 25). In Table 1 an overview of the fungi found in compost is presented. The course of fungal succession may be partially explained by the ecophysiological data available (7, 10, 14, 27–29). The typical pioneers *Rhizomucor* spp. and *Aspergillus fumigatus* have pH optima just below 7, and the temperature optimum of *Aspergillus fumigatus* is about 40°C. When self-heating and ammonification start and the pH reaches 9, the pioneers disappear. *Talaromyces thermophilus* and *Thermomyces lanuginosus* have relatively high pH and temperature optima. Their high thermal death points give a selective advantage in the period of maximum heat production. They do not degrade cellulose and have a moderate growth rate. *Scytalidium thermophilum* (synonyms, *Humicola grisea* var. *thermoidea*, *Humicola insolens*, and *Torula thermophila* [37]) and *Chaetomium thermophilum* grow fast and degrade cellulose strongly. However, *S. thermophilum*, in particular isolates of conidial type 2 with chains of conidia in the aerial mycelium (37), is the climax species. The number of CFU of *S. thermophilum* in fresh matter of phase II compost is about 10^6 g^{-1} (3, 6, 21, 23). The density of *S. thermophilum* in compost was found to be positively correlated with mushroom yield (35), and *S. thermophilum* strongly stimulated the extension rate of growth of mushroom mycelium (36).

This study is part of a program aimed to develop a method(s) for the production of compost of constant high quality that does not emit ammonia and odor into the environment (8, 19, 20). In order to intervene in compost microbiology, we consider the artificial inoculation and controlled preparation of compost. Here we report the selection of isolates of *S. thermophilum* and of other thermophilic fungi for their ability to promote mycelial growth of *A. bisporus* in sterilized compost. Because isolates of *S. thermophilum* degenerate easily (26, 37), full dependence on cultures from collections was avoided. We surveyed composts and isolated many *S. thermophilum* cultures and as many species of thermophilic fungi as possible.

MATERIALS AND METHODS

Substrate. Ingredients for composting were straw-bedded horse manure, wheat straw, broiler chicken manure, gypsum, and drainage from compost or water. Ingredients and composts were obtained from a commercial compost yard/tunnel plant. Some composts were prepared in our tunnel pilot plant (20). Then the ingredient mixture or the preparation scheme for mixing ingredients for phase I and phase II was occasionally simplified, horse manure was omitted as an ingredient, and/or phase I was skipped in processing (19, 20). We used the term "young compost" for any substrate prior to phase II. We also surveyed about 20 samples of self-heated pigpen litter (39).

Counting and isolation. Either diluted compost suspensions or washed compost particles (6) were plated in yeast-glucose agar containing penicillin and streptomycin (both 50 μg $liter^{-1}$) (35). Plates were incubated at 45°C in the dark and were screened daily for up to 5 days. Occasionally subcultures were made for microscopic identification. To avoid contamination

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TABLE 1. Thermophilic fungi found in mushroom compost[a]

Fungus	Reference(s)	Detected in this study[b]
Zygomycetes		
Absidia corymbifera	2, 6	+
Rhizomucor miehei	9	+
Rhizomucor pusillus	2–4, 6, 9, 12, 17, 21, 30	+
Ascomycetes		
Chaetomium thermophilum	2–4, 6, 9, 12, 17, 30	–
Corynascus thermophilus	15	+
Emericella nidulans	2, 4	+
Talaromyces emersonii		+
Talaromyces thermophilus	6, 9, 12	+
Thermoascus aurantiacus	3	+
Thermoascus aurantiacus var. *levispora*		+
Thermoascus crustaceus		+
Basidiomycete		
Coprinus cinereus		+
Hyphomycetes		
Aspergillus fumigatus	2–4, 6, 9, 12, 17, 21, 23, 30	+
Hormographiella aspergillata		+
Malbranchea sulfurea	6, 9	+
Paecilomyces variotii		+
Scytalidium thermophilum	2–4, 6, 9, 12, 17, 21, 23, 30	+
Stilbella thermophila	4, 12, 21, 30	+
Thermomyces lanuginosus	2–4, 6, 9, 12, 17, 21, 23, 30	+
Mycelia Sterilia		
Myriococcum thermophilum	3, 13	+
Miscellaneous[c]		
Thielavia terrestris		*
Chaetomium sp.		+
Basidiomycete		*
Undescribed taxon		+

[a] The nomenclature of reference 5 was followed.
[b] –, not found; +, isolated from compost (includes the eventual isolation from other substrates); *, isolated from horse droppings, not found in compost.
[c] Species isolated from horse droppings or not fully identified.

of the laboratory and its attendant health risks, *Rhizomucor*, *Absidia*, and *Aspergillus* colonies were not examined further. Representative cultures were kept on agar slants at room temperature and were subcultured twice a year.

Thermophilic fungi tested. The selection of isolates was started with 34 species, i.e., the 22 species mentioned in Table 1, our isolates from self-heated pigpen litter (*Chaetomium thermophilum*, *Mortierella wolfii*, *Rhizopus rhizopodiformis*, *Thermoascus thermophilus*, and a [second] basidiomycete), and *Corynascus sepedonium* CBS 223.81, *Humicola hyalothermophila* CBS 454.80, *Melanocarpus albomyces* CBS 747.70, *Scytalidium indonesiacum* CBS 259.81, *Thermomyces stellatus* CBS 272.61, *Thielavia heterothallica* CBS 117.65, and *Thielavia terricola* CBS 313.31. Of 20 species, 2 isolates were tested; of *Rhizomucor miehei*, *Rhizomucor pusillus*, *Rhizopus rhizopodiformis*, *Thermoascus thermophilus*, the two unidentified basidiomycetes, and the above-mentioned species from the Centraalbureau voor Schimmelcultures (CBS) collection, only one isolate was tested. For *S. thermophilum*, testing began with 42 of our isolates supplied with cultures from collections: ATCC 16453, 16454, and 16463; IMI 121649 and 131012; and CBS 147.64, 183.64, 183.81, 184.64, 225.63, 226.63, and 227.63.

Growth promotion of *A. bisporus*. Dried and ground (10-mm mesh) phase II compost was wetted, sterilized, and incubated for 3 to 5 days at 45°C with the thermophilic fungus to be tested. Growth tests with *A. bisporus* were done either in tubes or in dishes at 24°C to determine the mycelium extension rate (35) or the duration of the adaptation period of growth (36).

Presentation of data. Calculations were done with data from independent experiments; their number is indicated by *n*. Means and pooled standard deviations were calculated by analysis of variance by using GENSTAT 5 (24). Least significant differences between pairs of means depend on *n*. Since *n* varied, numerous least-significant-difference values can be calculated from standard deviations. For convenience we indicated significant differences where appropriate.

RESULTS AND DISCUSSION

Survey. The species of thermophilic fungi isolated (Table 1) represent most of the known thermophilic taxa. The identification of some isolates producing only sterile mycelium proved to be problematic. Some resembled *Chaetomium* spp., whereas others showed a basidiomycetous affinity. Isolates which belong to an undescribed taxon are to be investigated further. Fast-growing species were very common, and after 1 day of incubation, counting was possible only if the number of colonies per dilution plate was as small as 20. Therefore high dilutions were used. Macroscopically, young cultures of *S. thermophilum* resembled *Chaetomium thermophilum*; both were fast growing. *Rhizomucor* spp. and *Absidia corymbifera* were also very similar and fast growing. Colonies of *Talaromyces thermophilus* resembled *Thermomyces lanuginosus*; both had a moderate growth rate and appeared after 2 or 3 days of incubation.

Straw and drainage of compost were dominated by fast-growing and rapidly sporulating fungi, such as *Aspergillus fumigatus*, *Rhizomucor* spp., and *Absidia corymbifera*. *Talaromyces thermophilus* and *Thermomyces lanuginosus* were present at moderate densities, and *Corynascus thermophilus* and *S. thermophilum* were present at low densities. During phase I, total counts decreased (Table 2). Most species almost disappeared, but *S. thermophilum* was not much affected and seemed the exclusive species after phase II composting. After incubation of samples of phase II compost for 2 h at 70°C, *S. thermophilum* was hardly found in plate dilutions; however *Talaromyces thermophilus* and *Thermomyces lanuginosus* appeared, indicating that they were usually overlooked. Fungi recovered from washed phase II compost particles were almost exclusively *S. thermophilum*. Cultures were mostly of spore type 2 (37), having aerial conidia in long chains. In some cases, mixed cultures of *S. thermophilum* and a slow-growing yellow-green unidentified *Chaetomium* sp. developed. Then the colonies of *S. thermophilum* were yellowish in the center. The *Chaetomium* sp. could not be isolated from these mixed cultures but was occasionally isolated from particles remaining free of *S. thermophilum*. *Chaetomium* sp. was not isolated from compost from tunnels of a commercial compost yard. This may be caused by a larger temperature gradient which developed in the compost from bottom to top in our experimental tunnels compared with commercial tunnels. In the top of the compost *S. thermophilum* was suppressed and *Chaetomium* sp. was particularly abundant. If phase II composting had been started with ingredient mixtures that had hardly self-heated, recovery of *S. thermophilum* from washed particles was sometimes low. The normal count for compost from commercial tunnels was 100% (35).

Thielavia terrestris was isolated only from horse droppings. *Coprinus cinereus*, *Emericella nidulans*, *Malbranchea sulfurea*, *Paecilomyces variotii*, *Stilbella thermophila*, *Thermoascus au-*

TABLE 2. Numbers of thermophilic fungi in mushroom compost at its several stages of preparation

Source of fungi	Log_{10} CFU g^{-1}[a]	*S. thermophilum* frequency	*n*	*S. thermophilum* recovery (%)[a,b]	*n*
Wheat straw	3.4	Infrequent	6	ND[c]	
Drainage from compost	3.9	Infrequent	2	ND	
Horse droppings	2.3	Infrequent	3	ND	
Ingredient mixtures, start self-heating	3.3	Half	26	28	3
End phase I	2.4	Abundant	12	3	8
End phase II	6.5	Exclusive	5	90	54

[a] Standard deviations of CFU counts and of recovery are 1.00 and 17.3, respectively. Compared with data of ingredient mixtures, CFU counts and recovery were significantly lower at the end of phase I and higher at the end of phase II.
[b] Counts of fungal recovery from washed particles are restricted to *S. thermophilum*.
[c] ND, not determined.

rantiacus, *Thermoascus crustaceus*, and the undescribed taxon were very rarely found on straw or substrate mixtures starting to self-heat. *Myriococcum thermophilum* was isolated only once from compost. *Chaetomium thermophilum* was reported to be quite common in mushroom compost (Table 1), but we did not find it. However, we found *Chaetomium thermophilum* in samples of self-heated pigpen litter. These samples also provided us with additional isolates of *Malbranchea sulfurea* and *Myriococcum thermophilum* and with *Mortierella wolfii*, *Rhizopus rhizopodiformis*, *Thermoascus thermophilus*, and a basidiomycetous isolate. Some isolates of *Chaetomium thermophilum* and most isolates of *Thermoascus aurantiacus* died in our collection. La Touche (22) had observed the same for *Chaetomium thermophilum* and advised keeping it on straw; we maintained it successfully on compost agar.

Our survey provided us with valuable isolates of thermophilic fungi. Important ones were included in the CBS collection. *S. thermophilum* was very common. It has also been found in other composts (40), soil (38), and air (11). It grows very fast, and even CFU numbers below our detection limit of 1 g^{-1} are sufficient for rapid colonization of the substrate under favorable growth conditions. This means that when inoculum experiments with selected isolates are performed, adequate pasteurization of compost is required.

Growth promotion of *A. bisporus*. On sterilized compost in tubes, *A. bisporus* grew at a rate of 3.2 mm day^{-1} (Table 3). On nonsterilized phase II compost, in which *S. thermophilum* was dominant, growth occurred at 8.6 mm day^{-1} (35). All 54 isolates of *S. thermophilum* tested promoted growth of *A. bisporus* to rates of about 7 mm day^{-1} (37). Of 33 other species, 10 promoted growth of *A. bisporus* to rates above 5 mm day^{-1} (Table 3). This finding indicates some specificity of the growth-promoting factor(s). *Chaetomium thermophilum*, *Chaetomium* sp., *Malbranchea sulfurea*, *Myriococcum thermophilum*, and one of the unidentified basidiomycetes induced rates above 6 mm day^{-1}, like *S. thermophilum*. *A. bisporus* was also grown in dishes, and the effect of 21 isolates of *S. thermophilum* was tested. Isolate 15.8 caused an irregular start of growth. As a result, the period of growth adaptation lasted 13 days (36). Isolates IMI 131012, CBS 184.64, and CBS 227.63, as well as isolates 15.1 and M7.5.1, both belonging to a subtype of spore type 2 which also has short terminal chains of aerial conidia (37), caused regular growth, and the adaptation period was up to 3 days shorter (data not shown; differences just below significance).

The 10 species and the above-mentioned *S. thermophilum* isolates seemed interesting for inoculation for more controlled preparation of the substrate for *A. bisporus*. The two basidiomycetes grow very slowly and hence will need too much time to colonize compost. The fast-growing species, *S. thermophilum*, *Chaetomium thermophilum*, and *Myriococcum thermophilum*, appear the most promising.

TABLE 3. Growth rates of *A. bisporus* on sterilized compost inoculated with different thermophilic fungi

Species	Isolate designation	Source	Mycelial extension rate K_r (mm/day)[a]	*n*
None (sterile control)	-		3.2	44
Chaetomium thermophilum	209.3	Pigpen litter	6.1	2
	T49.6.5	Pigpen litter	6.9	2
Chaetomium sp.	M4.7	Mushroom compost	7.9	3
	98.5	Mushroom compost	6.9	2
Corynascus sepedonium	CBS 223.81		6.4	2
Malbranchea sulfurea	T20.1	Mushroom compost	7.1	2
	T49.9.1	Pigpen litter	6.4	2
Myriococcum thermophilum	82.2.9 (CBS 208.89)	Mushroom compost	7.1	3
	T49.6.6	Pigpen litter	6.3	2
Scytalidium thermophilum	15.8 (CBS 671.88)	Mushroom compost	7.2	39
Stilbella thermophila	82.4.3a	Mushroom compost	5.1	2
	200.3	Mushroom compost	5.4	3
Thielavia heterothallica	CBS 117.65		5.6	2
Thielavia terrestris	T104.1.2	Horse droppings	5.3	2
	244.3.7	Horse droppings	5.0	2
Basidiomycete 1	244.3.8	Horse droppings	6.9	2
Basidiomycete 2	242.2.1	Mushroom compost	5.8	3

[a] Standard deviation of K_r is 0.84. All isolates caused a significantly higher K_r than the control. However, values below 6 were significantly below 7.2, the value obtained by treatment with *S. thermophilum* isolate 15.8.

Tests on promotion of *A. bisporus* growth with actinomycetes and other bacteria have been negative (35). However, after incubation of samples of phase II compost for 10 min at 100°C, for the selective inactivation of fungi, fast growth of *A. bisporus* was found. Subculturing this substrate into sterilized compost also resulted in fast growth of *A. bisporus*, although the adaptation period was extended by 6 days. After seven "generations" of subculturing, the growth-promoting effect was still present. However, none of the prokaryotes isolated thus far from these substrates was growth promoting. Stanek (33) found that *A. bisporus* growth on a substrate incubated with a mixture of a *Pseudomonas* sp. and a *Streptomyces* sp. was satisfactory, while incubations with the species alone were not.

The growth-promoting species are not pioneers of compost. Probably they are all cellulolytic. However, *Aspergillus fumigatus* and *Corynascus thermophilus* are cellulolytic but do not promote growth. Growth promotion is limited to the rate of extension of *A. bisporus* mycelium, the specific rate of biomass increase not being affected. We failed in our attempt to further elucidate the growth-promoting effect (34). Stanek (32) reported that filtrates of fungal, actinomycetal, and other bacterial cultures stimulated biomass growth of *A. bisporus* mycelium. Recently, the involvement of CO_2 has been reported (42).

The selected species will be further investigated for inoculation and controlled preparation of compost.

ACKNOWLEDGMENTS

We thank J. A. M. Voermans and T. Greutink, Research Institute for Pig Husbandry, Rosmalen, The Netherlands, for samples of self-heated pig-pen litter, and K. B. Uljé, Alphen aan de Rijn, The Netherlands, and J. Guarro, University of Barcelona, Barcelona, Spain, for identifying *Coprínus cinereus* and *Hormographiella aspergillata*, respectively.

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