

A survey of bacteria and fungi occurring during composting and self-heating processes

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Abstract - Composting is a controlled self-heating, aerobic solid phase biodegradative process of organic materials. The process comprises mesophilic and thermophilic phases involving numerous microorganisms. In several successive steps, microbial communities degrade organic substrates into more stable, humified forms and inorganic products, generating heat as a metabolic waste product. Due to the complexity of substrates and intermediate products, microbial diversity and the succession of populations is a prerequisite to ensure complete biodegradation. Due to the dynamic process, both in time and space (microhabitats), which is reflected by constantly changing pH, humidity, oxygen partial pressure and temperature it is extremely difficult to detect, albeit isolate, all the microorganisms involved. Research on composts is also so difficult because the process can hardly be simulated in the laboratory since all major gas and temperature fluxes are to a large extent determined by the physical extension of the system. In this comprehensive survey of literature an inventory of the mesophilic and thermophilic bacteria, actinomycetes and fungi isolated during several phases of composting (including also self-heating organic materials) is presented.

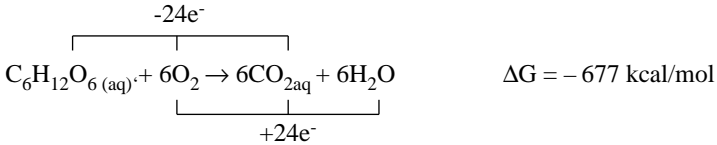
Key words: self-heating material, compost, microbial diversity, bacteria, actinomycetes, fungi, degradation.

INTRODUCTION

Composting is, *sensu stricto*, a self-heating, aerobic solid phase biodegradative process of organic materials under controlled conditions, which distinguishes it from natural rotting or putrefaction. From an etymological viewpoint, *lat. compositum*, it is a mixture of substrates that is biodegraded by a mixed microbial

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community. The 'self-heating' is due to heat liberation from microbial metabolic activity:



The heating-up during a composting process is determined by the degradability and energy content of the substrates, the availability of moisture and oxygen, and the mode of energy conservation (insulation, convective losses) (Finstein and Morris, 1975; Haug, 1993).

The organic substrates and bulking agents used in composting are mainly derived from plant material. Carbon compounds serve as an energy source for microbial maintenance and growth. The yield coefficient, that is the amount of C incorporated into the cells per unit degraded C, ranges from 10% to 35%, depending on substrate energy content, degrading organism and environmental conditions.

Besides a C source, microorganisms require macronutrients such as N, P and K, and trace elements for their growth. Nitrogen is a critical element for microbial growth. If N is limiting during composting the degradation process will be slow. At excess supply, N may be lost from the system as ammonia gas or through leaching as nitrate. If we assume a microbial yield coefficient of 30%, and an average microbial C/N content of 10, the theoretical optimum substrate C/N ratio would be 30. Indeed, in practice the optimum C/N ratio has been reported to range between 25 and 35 (Shilesky and Maniotis, 1969; Gray *et al.*, 1971; Savage *et al.*, 1973; Finstein and Morris, 1975; de Bertoldi *et al.*, 1985; Fogarty and Tuovinen, 1991; Golueke, 1991, 1992; Larsen and McCartney, 2000; Tuomela *et al.*, 2000). During the process the C/N ratio decreases significantly (see Figure 1) (Thambirajah *et al.*, 1995) because part of the C is lost as CO₂ upon microbial respiration while N is recycled (Shilesky and Maniotis, 1969; Golueke, 1992).

Decomposition by microorganisms occurs predominantly in the thin liquid films (biofilms) on the surface of the organic particles. If the moisture content drops below a critical level (<30%), microbial activity will decrease and the microorganisms will become dormant. On the other hand, a moisture content that is too high (>65%) can cause oxygen depletion and losses of nutrients through leaching. In subsequent anaerobic conditions the decomposition rate decreases and odor problems arise (de Bertoldi *et al.*, 1985; Fogarty and Tuovinen, 1991; Golueke, 1991; Tiquia *et al.*, 1996). However, even under optimal conditions, anaerobic microenvironments may develop. For example, Atkinson *et al.* (1996c) estimated that almost 1% of all the bacteria found in municipal solid waste compost are anaerobic.

Under optimal conditions the composting process can be divided into four phases: (i) an initial (first) mesophilic phase (10-42 °C), which may last for only a few hours or a couple of days; (ii) a thermophilic phase (temperature 45-70 °C), lasting a few days, several weeks (particularly in food wastes) or even months (particularly in wood wastes); (iii) second mesophilic phase during which mesophile organisms, often dissimilar to those of the first mesophilic phase, recolonize the substrates; and (iv) the maturation (or curing) and stabilization phase which can last for several weeks to several months (Hoitink and Boehm, 1999;

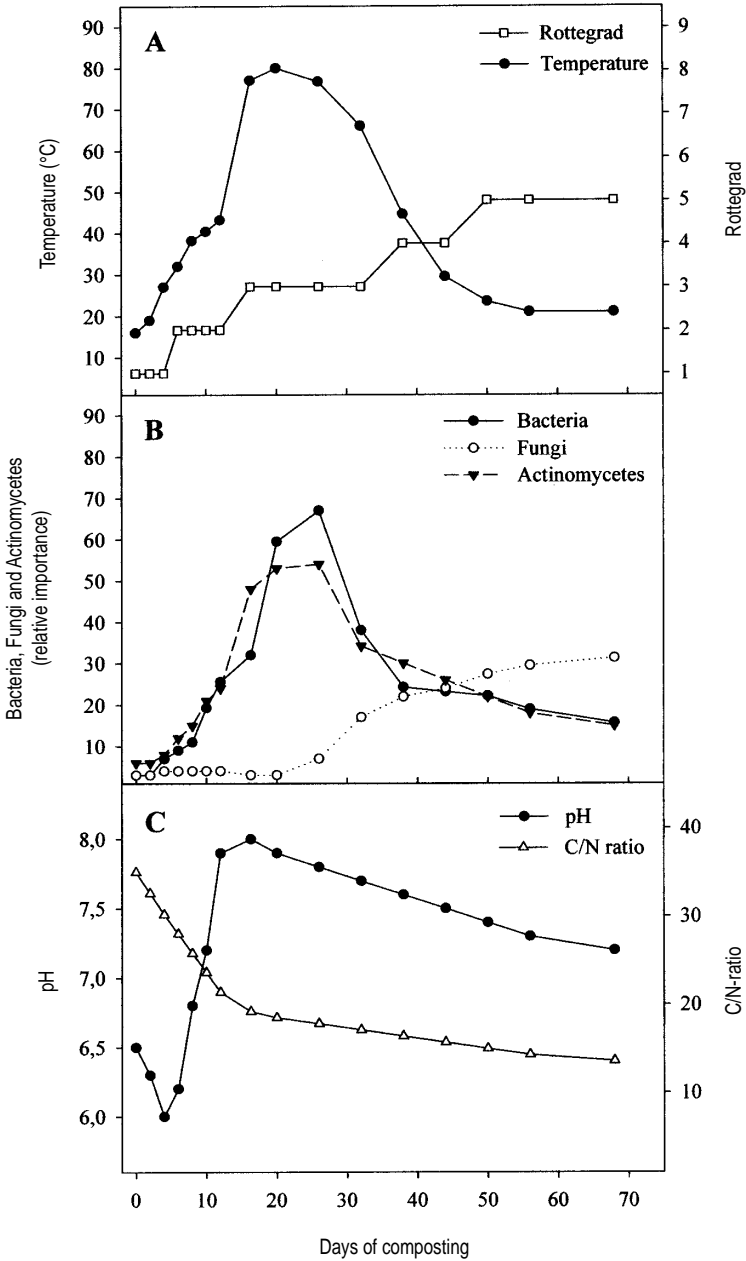


FIG. 1 – Typical process parameters and microbial abundance during composting. These curves, including extension of the time axis, may vary to a great degree depending on factors such as substrate, outside temperature, moisture availability and type of aeration or turning frequency.

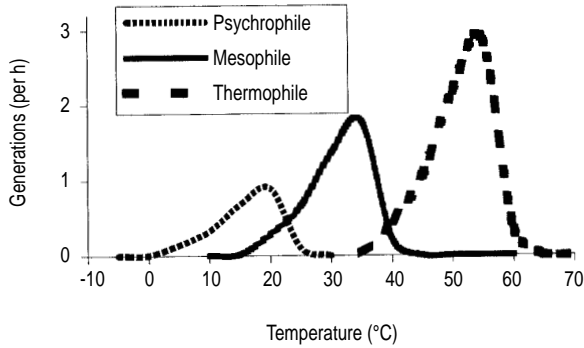


FIG. 2 – Temperature range of psychrotolerant, mesophile and thermophile organisms, and their generation time (from: Insam and de Bertoldi, 2003).

Tuomela *et al.*, 2000; Insam and de Bertoldi, 2003). These phases may have considerable overlap based on temperature gradients and differential temperature effects on microorganisms (Fogarty and Tuovinen, 1991).

Different microbial communities predominate during the various composting phases, each of which being adapted to a particular environment (Gray *et al.*, 1971; Bagstam, 1978; Crawford, 1983). Primary decomposers create a physico-chemical environment suited for secondary organisms, which cannot attack the initial substrates, while metabolites produced by the one group can be utilized by the other (crossfeeding) (Davis *et al.*, 1992; Golueke, 1992). The initial rapid increase of temperature involves a rapid transition from mesophilic to thermophilic microflora (Niese, 1959; Corominas *et al.*, 1987; Falcon, 1987; Ryckeboer *et al.*, 2003). Often, however, a disruption of the process is observed at temperatures between 42 °C and 45 °C. The initial mesophilic microflora is inhibited by the high temperature, while the thermophilic populations have not yet developed and are below their temperature optimum (see Figure 2). Only after a sufficient number of thermophiles is generated, temperatures rise again. At temperatures exceeding 60 °C, the optimum for most thermophiles is reached, and the system starts to limit itself due to the inhibitory high temperatures (McKinley and Vestal, 1984). Heat may *per se* inhibit organisms (e.g. through enzyme inactivation) or may limit oxygen supply (O₂ solubility in water is temperature dependent). If a good management is provided (i.e. regular aeration or frequent turning), the thermophilic stage continues until the heat production becomes lower than the heat dissipation, due to the exhaustion of easily degradable substrates. High temperatures support degradation of recalcitrant organics such as lignocellulose, e.g. wood (Sjöström, 1993; Tuomela *et al.*, 2000) and elimination of pathogenic and allergenic microorganisms (Wiley and Westerberg, 1969; Finstein and Morris, 1975; Bollen, 1993; Herrmann *et al.*, 1994; Thambirajah *et al.*, 1995; Beffa *et al.*, 1996a, 1996b; Bollen and Volker, 1996; Ryckeboer *et al.*, 2002a). During the second mesophilic (cooling) phase nutrients become a limiting factor, causing a decline in microbial activity and heat output. During the maturation phase, the substrate quality further declines and compounds such as lignin-humus complexes are formed that are not further degradable.

The length of the different composting phases depends on the nature of the organic matter being composted and the efficiency of the process, which is determined by several factors such as starting material, O₂ supply, moisture content, active turning and outside temperature.

Although composting is an ancient art, and very often works by itself, more knowledge on the involved microbiota will help to improve the process, both regarding its progress and the quality of the end-products that may be obtained.

Enumerations and isolations of microorganisms from composts have mostly been performed on rich organic complex media (Kane and Mullins, 1973; Finstein and Morris, 1975; Nakasaki *et al.*, 1985a, 1985b; Strom 1985a, 1985b; Hardy and Sivasithamparam, 1989; Davis *et al.*, 1991; Beffa *et al.*, 1996b; Choi and Park, 1998; Ryckeboer *et al.*, 2003; Van Gestel *et al.*, 2003). Later, techniques such as measuring of ATP content (Garcia *et al.*, 1992; Tseng *et al.*, 1996), microbial biomass (Derikx *et al.*, 1990) and of potential metabolic abilities such as metabolic fingerprinting became available (Insam *et al.*, 1996; Kersters *et al.*, 1997). More recently, methods have been introduced that do not require cultivation, e.g. direct analysis of phospholipid fatty acid (PLFA) (Hellmann *et al.*, 1997; Herrmann and Shann, 1997; Klamer and Baath, 1998) or DNA and RNA extraction (Hugenholz *et al.*, 1998; Koschinsky *et al.*, 1998; Gurtner *et al.*, 2000; Ivors *et al.*, 2000; Alfreider *et al.*, 2002). Denaturing Gradient Gel Electrophoresis (DGGE) of PCR-amplified DNA fragments combined with the sequencing of relevant bands, Terminal Restriction Fragment Length Polymorphism analysis (T-RFLP) of 16S (prokaryotes) or 18S (eukaryotes) rDNA genes and amplified ribosomal DNA restriction analysis (ARDRA) are examples of the most recent methodological developments in PCR-based detection techniques to analyze the diversity of microbial communities in self-heating materials (Ivors *et al.*, 2002; McSpadden-Gardener *et al.*, 2002; Michel *et al.*, 2002; Minz *et al.*, 2002; Riddech *et al.*, 2002; Roberts *et al.*, 2002; Alfreider *et al.*, 2002; Tiquia and Michel, 2002; Tiquia *et al.*, 2002). The use of growth requiring culturing techniques is often disputed, while the culture-independent molecular screening techniques will definitely detect numerous unique microorganisms. Nevertheless, a few references clearly indicate that culturing studies still deliver non-overlapping information, consequently none of the two approaches can claim to be superior to the other yet (Brambilla *et al.*, 2001).

MICROBIAL COMMUNITIES DURING COMPOSTING

Substrates and communities

Quantitatively, the main components of organic matter are carbohydrates (e.g. cellulose), proteins, lipids and lignin (as presented in Table 1). The capacity of microorganisms to assimilate organic matter depends on their ability to produce the enzymes needed for degradation of the substrate (Golueke, 1991, 1992; Davis *et al.*, 1992; Tuomela *et al.*, 2000). The composition of the microbial community during composting is determined by many factors (Davis *et al.*, 1992; Golueke, 1992). Under aerobic conditions, temperature is the major selective factor for populations and determines the rate of metabolic activities. The reports on the number of organisms during the different phases of composting are contradictory (Table 2). While some authors state that the total number of microorganisms does not significantly

TABLE 1 – Major natural compounds which are the substrates for decomposition. These materials are found in plants animals and microorganisms. From: Insam and de Bertoldi (2003)

Compound	Composition	Function	P*	A*	M*	Degradability
Lignin	Polymerisates of phenylpropane derivatives, e.g. coniferyl alcohol	Structural compound	3	0	0	Very resistant, mainly by fungi
<i>Glucose (C₆H₁₀O₅)_n polymers</i>						
Cellulose	β -1,4 bonds	Structural compound (plant leaves, stems)	3	0	0	Easily, mainly by fungi, but also bacteria, Actinomycetes
Starch	Amylose: linear α -1,4 bonds; Amylo-pectin: branched α -1,4 bonds	Storage compound in seeds and roots	2	0	1	Good; Aerobically and anaerobically (<i>Clostridium</i>)
Glycogen	α -1,4 and α -1,6 bonds	In animal muscles	0	1	0	Good
Laminarin	β -1,3 bonds	Marine algae (Phaeophyta)	2	0	0	Fair
Paramylon	β -1,3 bonds	Algae (Euglenophyta and Xanthophyta)	1	0	0	Fair
Dextran	1,6 bonds	Capsules or slime layers of bacteria	0	0	1	Fair
Agar	Polymer of Galactose and galacturonic acid	Marine algae (Rhodophyta)	2			Resistant
Suberin, cutine	High polymeric esters of saturated and unsaturated fatty acids	Structural compound	1	0	0	Poor
<i>Hemicelluloses</i>						
Xylan	Low degree of polymerisation of sugar monomers (Pentoses and Hexoses) and Uronic acids; usually 20-100 monomers	Cell wall compound, in seeds, straw, wood, algae	3	0	0	Variable degradability, often together with lignin
Araban						
Mannan						
Galaktan						

(continued)

TABLE 1 – Major natural compounds which are the substrates for decomposition. These materials are found in plants animals and microorganisms. From: Insam and de Bertoldi (2003) (follow the previous page)

Compound	Composition	Function	P*	A*	M*	Degradability
Pectin	Polymer of galacturonic acids (3 10 ⁴ -5 10 ⁵ monomers)	Dissolved, and in the cell wall, in seeds, fruits, and in young wood parts	2	0	0	Easy, by most microorganisms, among them often plant pathogens
Sucrose	Glucose-fructose disaccharide	Vacuoles	2	0	1	Very easy by most microorganisms
Lactose	Glucose-galactose disaccharide	Milk	0	1		Easy by lactic acid bacteria
Hyaluronic acid	Polysaccharide of glucuronic acid and N-acetylglucosamine	Connective tissue	0	1	0	Easy
Chlorophyll and other Pigments		Plastids	1	0	0	Easy
Alkaloids, tannins,	Sugars, mainly alpha-D-glucose	Vacuoles	1		0	Variable
Fats, waxes	Glycerine and fatty acids	Storage compound	1	3	1	Variable
DNS, RNS	Nucleic acids	Nuclei, Mitochondria	1	1	2	Easy
Poly-β-hydroxy butyric acid		Vacuoles, storage compound	0	0	2	Easy
Murein	Peptidoglycan	Cell wall of bacteria	0	0	3	Easy

* P: plants, A: animals, M: microorganisms. Figures indicate the relative importance (0... not found; 3... found in very high quantities).

TABLE 2 – Approximate numbers of microorganisms during different phases of composting (after Miller, 1993)

Organism	Number
Bacteria in mesophilic stage	10^9 - 10^{13} g ⁻¹ substrate
Bacteria in thermophilic stage	10^8 - 10^{12} g ⁻¹ substrate
Actinomycetes, thermophilic stage	10^7 - 10^9 g ⁻¹ substrate
Actinomycetes, mesophilic stage	10^8 - 10^{12} g ⁻¹ substrate
Fungi*, average value	10^5 - 10^8 g ⁻¹ substrate

* Due to the mycelial growth, actinomycete and fungal numbers are ambiguous.

change during composting (Atkinson *et al.*, 1996a), other authors report higher numbers for the mesophilic stage. There is agreement, however, that the composition of the community can vary during the different phases of the composting process (Atkinson *et al.*, 1996a; Ryckeboer *et al.*, 2003). Only few studies describe the diversity of prokaryotes and/or fungi during an entire composting process. For example, Von Klopotek (1962) and Breitenbach (1998) examined the fungal diversity during the composting of (source-separated) municipal solid waste, while Strom (1985a, 1985b) and Beffa *et al.* (1996b) determined the diversity of prokaryotes during the composting of (source-separated) municipal solid wastes. Ryckeboer *et al.* (2003) examined diversity and population densities of prokaryotes and fungi throughout the whole composting process of source-separated household wastes, i.e. from starting material to mature compost. Since starting material and process conditions determine the community composition to a large degree, it is difficult to generalize. Below, it is attempted to summarize the most typical microbial features that characterize composting processes.

Starting phase - first mesophilic phase

Due to the heterogeneity of substrates, little is known on the original composition of the waste microbial community. Only few authors report on microbial diversity present in organic waste material. Von Klopotek (1962) isolated few mesophilic fungi from fresh municipal solid waste at a temperature of 36 °C. Ryckeboer *et al.* (2003) found few mesophilic fungi in source-separated household waste, but numerous thermophilic fungi and bacteria. During the initial phase of the composting process the substrates are at ambient temperature and the pH is usually slightly acidic (Figure 1). Mesophilic and/or thermotolerant fungi and bacteria are the dominant active degraders of fresh organic waste materials (20-40 °C). Food wastes containing vegetable residues often have a low initial pH (4.5 to 5.0), which stimulates the proliferation of fungi and yeasts (Choi and Park, 1998; Ryckeboer *et al.*, 2003). These microorganisms rapidly break down soluble and easily degradable carbon sources, resulting in a pH drop due to organic acids (Stutzenberger *et al.*, 1970; Gray *et al.*, 1971, Finstein and Morris, 1975; Beffa *et al.*, 1996b).

Ammonification causes an increase of pH favourable for bacteria that subse-

quently out-compete fungi within a few hours or days. The high surface/volume ratio of bacteria allows a rapid transfer of soluble substrates into the cell. Bacteria are nutritionally also the most diverse group of compost organisms, using a broad range of enzymes to chemically degrade a variety of organic materials. Also, the average generation time of bacteria is much shorter than that of fungi which gives them a competitive advantage during those phases of the composting process that are characterized by rapid changes in substrate availability and other process parameters (temperature, moisture, aeration etc.). As a result, numbers of bacteria (including actinomycetes) are usually much higher than numbers of other microorganisms, e.g. fungi (if total numbers are comparable at all). Consequently, bacteria are responsible for most of the initial decomposition and heat generation in compost, provided that the major growth requirements are met. For bacteria, the optimal moisture content ranges from 50 to 60% (Fogarty and Tuovinen, 1991; Golueke, 1992), and they favor a near-neutral pH.

Actinomycetes develop more slowly than most bacteria and fungi and are rather ineffective competitors when nutrient levels are high (Lacey, 1973; Hardy and Sivasithamparam, 1989; Beffa *et al.*, 1996b; Hoitink and Boehm, 1999). A wide range of prokaryotes produce amylase enzymes which enable them to degrade starch (Table 3), also important during the initial phase (Fagan and Fergus, 1984; Diaz-Ravina *et al.*, 1989; Domsch *et al.*, 1993; Atkinson *et al.*, 1996b).

TABLE 3 – Overview of prokaryotes reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures

Organism*	Temperature phase**	Source material***	Reference
<i>Achromobacter</i> sp.	m, t	U, W	Strauch and de Bertoldi (1985); Ogawa <i>et al.</i> (1964)
<i>Achromobacter xylosoxidans</i>	m	A	Mergaert, unpublished data
<i>Acidovorax facilis</i>	m	A	Mergaert <i>et al.</i> (1994a)
<i>Acidovorax</i> sp.	m	U	Mergaert and Swings (1996)
<i>Acinetobacter</i> sp.	m, t	A, U	Mergaert, unpublished data; Droffner <i>et al.</i> (1995)
<i>Actinomyces</i> sp. °	t	P, U	Waksman <i>et al.</i> (1939a); Golueke (1977)
<i>Alcaligenes faecalis</i>	m, t	U, V	Corominas <i>et al.</i> (1987); Droffner <i>et al.</i> (1995)
<i>Alcaligenes</i> sp.	m	P, Y	Masanori and Kazuo (1998); Rocha <i>et al.</i> (2002)
<i>Amphibacillus xylanus</i>		I	Nimura <i>et al.</i> (1990)
<i>Arthrobacter ilicis</i> °	m	U	Mergaert <i>et al.</i> (1994a); Mergaert and Swings (1996)
<i>Arthrobacter</i> sp. °	m	A, V	Corominas <i>et al.</i> (1987); Beffa <i>et al.</i> (1996b)
<i>Azotobacter</i> sp.	m	Y	Rocha <i>et al.</i> (2002)

(continued)

TABLE 3 – Overview of prokaryotes reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Bacillus amyloliquefaciens</i>	m, t	A	Ryckeboer <i>et al.</i> (2003)
<i>Bacillus badius</i>	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Bacillus cereus</i>	m	A, M, P, V	Corominas <i>et al.</i> (1987); Hoitink and Fahy (1986); Kaneshiro <i>et al.</i> (1995); Ryckeboer <i>et al.</i> (2003)
<i>Bacillus circulans</i>	t	D	Strom (1985b)
<i>Bacillus coagulans</i>	t	A, D, O	Fermor <i>et al.</i> (1979); Strom (1985b); Koschinsky <i>et al.</i> (1998); Mergaert, unpublished data
“ <i>Bacillus denitrificans</i> ”	t	O	Koschinsky <i>et al.</i> (1998)
<i>Bacillus licheniformis</i>	m, t	A, D, G, O	Strom (1985b); Ivors <i>et al.</i> (2000); Ryckeboer <i>et al.</i> (2003)
<i>Bacillus megaterium</i>	m, t	U, V	Corominas <i>et al.</i> (1987); Mergaert <i>et al.</i> (1994a); Mergaert and Swings (1996); Mergaert, unpublished data
<i>Bacillus mycoides</i>		M	Hoitink and Fahy (1986)
<i>Bacillus oleronius</i>	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Bacillus pallidus</i>	t	U	Blanc <i>et al.</i> (1997)
<i>Bacillus pumilus</i>	m, t	A, V	Corominas <i>et al.</i> (1987); Ryckeboer <i>et al.</i> (2003)
<i>Bacillus schlegelii</i>	t	A	Beffa <i>et al.</i> (1996a,1996b)
<i>Bacillus smithii</i>	t	A, O	Koschinsky <i>et al.</i> (1998); Ryckeboer <i>et al.</i> (2003)
<i>Bacillus</i> sp.	m, t	A, C, G, M, U, W, Y	Corominas <i>et al.</i> (1987); Hardy and Sivsithamparam (1989); Beffa <i>et al.</i> (1996b); Michel <i>et al.</i> (1997b); Blanc <i>et al.</i> (1998); Choi and Park (1998); Ogawa <i>et al.</i> (1998); Tuitert <i>et al.</i> (1998); Mannix <i>et al.</i> (2001); Rocha <i>et al.</i> (2002); Ryckeboer <i>et al.</i> (2003)
<i>Bacillus sphaericus</i>	m	A, D, N, V	Strom (1985b); Corominas <i>et al.</i> (1987); Seck and Kilbertus (1996); Ryckeboer <i>et al.</i> (2003)

(continued)

TABLE 3 – Overview of prokaryotes reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Bacillus subtilis</i>	m, t	A, D, M, N, O, R, U, V	Fermor <i>et al.</i> (1979); Strom (1985b); Hoitink and Fahy (1986); Corominas <i>et al.</i> (1987); Phae <i>et al.</i> (1990); Asaka and Shoda (1996); Nakasaki <i>et al.</i> (1996); Seck and Kilbertus (1996); Ryckeboer <i>et al.</i> (2003)
<i>Bacillus thuringiensis</i>	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Bacteroides</i> sp.	m	Y	Rocha <i>et al.</i> (2002)
<i>Bradyrhizobium</i> sp.		U	Mannix <i>et al.</i> (2001)
<i>Brevibacillus brevis</i> (syn.: <i>Bacillus brevis</i>)	t	D	Strom (1985b)
<i>Brevibacillus agri</i>	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Brevibacillus laterosporus</i> (syn.: <i>Bacillus laterosporus</i>)	m	U	Mergaert, unpublished data
<i>Brevibacillus thermoruber</i> (syn.: <i>Bacillus thermoruber</i>)	t	O	Manachini <i>et al.</i> (1985)
<i>Brevundimonas diminuta</i>	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Brevundimonas</i> sp.		U	Mannix <i>et al.</i> (2001)
<i>Caryophanon latum</i>	m	O	Ivors <i>et al.</i> (2000)
<i>Caulobacter</i> sp.		U	Mannix <i>et al.</i> (2001)
<i>Cellulomonas cellulans</i> °	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Cellulomonas flavigena</i> °	m	A	Ryckeboer, unpublished data
<i>Cellulomonas</i> sp.	m	Y	Rocha <i>et al.</i> (2002)
<i>Chromobacterium</i> sp.	m	O	Fermor <i>et al.</i> (1979)
<i>Chryseobacterium balustinum</i> (syn.: <i>Flavobacterium balustinum</i>)	m	M	Hoitink and Fahy (1986); Hoitink (1990)
<i>Chryseobacterium gleum</i> (syn.: <i>Flavobacterium gleum</i>)	m	P	Kaneshiro <i>et al.</i> (1995)
<i>Citrobacter freundii</i>	t	U	Droffner <i>et al.</i> (1995)
<i>Citrobacter</i> sp.	m	P, U	Strauch (1987); Masanori and Kazuo (1998)
<i>Clostridium</i> sp.	m	W, U, Y	Ogawa <i>et al.</i> (1964); Mannix <i>et al.</i> (2001); Rocha <i>et al.</i> (2002)
<i>Clostridium thermocellum</i>	t	P	Henssen (1957)
<i>Comamonas testosteroni</i>	m	U	Mergaert <i>et al.</i> (1994a); Mergaert and Swings (1996)
<i>Corynebacterium jeikeium</i> °	m	A	Andrews <i>et al.</i> (1994)

(continued)

TABLE 3 – Overview of prokaryotes reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Corynebacterium striatum</i> °	m	A	Mergaert, unpublished data
<i>Curtobacterium flaccunfaciens</i> °	m	A	Mergaert, unpublished data
<i>Cytophaga</i> sp.	m	P	Waksman <i>et al.</i> (1939a)
<i>Desulfotomaculum thermosapovorans</i>	t	U	Fardeau <i>et al.</i> (1995)
<i>Enterobacter cloacae</i>	t	M	Hoitink and Fahy (1986); Droffner <i>et al.</i> (1995)
<i>Enterobacter</i> sp.	m	P, Y, U, G	Strauch (1987); Masanori and Kazuo (1998); Rocha <i>et al.</i> (2002)
<i>Enterococcus gallinarum</i>		U	Droffner <i>et al.</i> (1995)
<i>Enterococcus</i> sp.		U	Strauch (1987)
<i>Escherichia coli</i>	m	U, G	Strauch (1987); Droffner <i>et al.</i> (1995)
<i>Flavimonas oxyzihabitans</i>	m	A	Andrews <i>et al.</i> (1994)
<i>Flavobacterium johnsoniae</i> (syn.: <i>Cytophaga johnsonae</i>)	m	U	Mergaert <i>et al.</i> (1994a); Mergaert and Swings (1996)
<i>Flavobacterium mizutaii</i>	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Flavobacterium</i> sp.	m	O	Fermor <i>et al.</i> (1979)
<i>Geobacillus stearothermophilus</i> (syn.: <i>Bacillus stearothermophilus</i>)	t	A, D, O, W	Fermor <i>et al.</i> (1979); Strom (1985b); Fujio and Kume (1991); Ryckeboer <i>et al.</i> (2003)
<i>Geobacillus thermodenitrificans</i> (syn.: <i>Bacillus thermodenitrificans</i>)	t	U	Blanc <i>et al.</i> (1997)
<i>Geobacillus thermoglucosidasius</i> (syn.: <i>Bacillus thermoglucosidasius</i>)	t	A, U	Blanc <i>et al.</i> (1997); Ryckeboer <i>et al.</i> (2003)
<i>Hydrogenobacter</i> sp.	t	A	Beffa <i>et al.</i> (1996a, 1996b); Blanc <i>et al.</i> (1998)
<i>Janthinobacterium lividum</i>		M	Hoitink and Fahy (1986)
<i>Klebsiella pneumoniae</i>	m, t	A, U	Droffner <i>et al.</i> (1995); Andrews <i>et al.</i> (1994)
<i>Klebsiella</i> sp.		G, U	Strauch (1987)
<i>Kocuria varians</i>	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Methanothermobacter thermoautotrophicus</i> (syn.: <i>Methanobacterium thermoautotrophicum</i>)	t	O	Derikx <i>et al.</i> (1989)
<i>Methylobacterium extorquens</i>	m	A	Andrews <i>et al.</i> (1994)
<i>Methylobacterium organophilum</i>	m	A	Ryckeboer <i>et al.</i> (2003)

(continued)

TABLE 3 – Overview of prokaryotes reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Methylobacterium</i> sp.		U	Mannix <i>et al.</i> (2001)
<i>Microbacterium flavescens</i> (syn.: <i>Aureobacterium flavescens</i> , <i>Arthrobacter flavescens</i>) °	m	N	Seck and Kilbertus (1996)
<i>Micrococcus luteus</i> °	m	A, N	Ryckeboer, unpublished data; Seck and Kilbertus (1996)
<i>Micromonospora</i> sp. °	t	P, U	Waksman <i>et al.</i> (1939a), Golueke (1977)
“ <i>Micromonospora vulgaris</i> ” °	t	F, K	Erikson (1952); Corbaz <i>et al.</i> (1963)
<i>Moraxella bovis</i>	m	A	Andrews <i>et al.</i> (1994)
<i>Nitrobacter</i> sp.	m	Y	Rocha <i>et al.</i> (2002)
<i>Nitrosomonas</i> sp.	m	Y	Rocha <i>et al.</i> (2002)
<i>Nocardia brasiliensis</i> °	t	O	Fergus (1964)
<i>Nocardia otitidiscaviarium</i> °	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Nocardia</i> sp. °	m, t	P, Y	Henssen (1957); Rocha <i>et al.</i> (2002)
<i>Paenibacillus lentimorbus</i>	m, t	A	Ryckeboer <i>et al.</i> (2003)
<i>Paenibacillus macerans</i>	m, t	A, O	Ospina-Giraldo <i>et al.</i> (1996); Ryckeboer <i>et al.</i> (2003)
<i>Paenibacillus pabuli</i>	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Paenibacillus polymyxa</i>	m	A, G	J. Ryckeboer, unpublished data; Ryckeboer <i>et al.</i> (2003)
<i>Pantoea agglomerans</i> (syn.: <i>Enterobacter agglomerans</i>)		M	Hoitink and Fahy (1986)
<i>Paracoccus denitrificans</i>	m	A	Beffa <i>et al.</i> (1996b); Ryckeboer <i>et al.</i> (2003)
<i>Paracoccus versutus</i> (syn.: <i>Thiobacillus versutus</i>)	m	A	Beffa <i>et al.</i> (1996b)
<i>Paucimonas lemoignei</i> (syn.: <i>Pseudomonas lemoignei</i>)	m	U	Mergaert <i>et al.</i> (1994a); Mergaert and Swings (1996)
<i>Phyllobacterium rubiacearum</i>	m	A	J. Mergaert, unpublished data
“ <i>Plectridia</i> ” sp.	t	P	Waksman <i>et al.</i> (1939a)
<i>Propionibacterium</i> sp.		U	Mannix <i>et al.</i> (2001)
<i>Proteus hauseri</i> (syn.: <i>Proteus vulgaris</i>)		U	Strauch (1987)
<i>Proteus mirabilis</i>		U	Strauch (1987)
<i>Pseudoaltermonas haloplanktis</i> (syn.: <i>Alteromonas haloplanktis</i>)	m	U	Mergaert and Swings (1996)

(continued)

TABLE 3 – Overview of prokaryotes reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Pseudomonas aeruginosa</i>		M	Hoitink and Fahy (1986)
<i>Pseudomonas alcaligenes</i>	m	A, U	Mergaert <i>et al.</i> (1994a); Mergaert and Swings (1996); Ryckeboer <i>et al.</i> (2003)
<i>Pseudomonas balearica</i>	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Pseudomonas fluorescens</i>	m	A, M	Hoitink and Fahy (1986); Andrews <i>et al.</i> (1994)
<i>Pseudomonas mendocina</i>	m	A, U	Mergaert and Swings (1996); J. Mergaert, unpublished
<i>Pseudomonas pseudoalcaligenes</i>	m	A, U	Droffner <i>et al.</i> (1995); J. Mergaert, unpublished
<i>Pseudomonas putida</i>	m	A, M	Hoitink and Fahy (1986); Andrews <i>et al.</i> (1994)
<i>Pseudomonas sp.</i>	m	A, G, M, O, P, U, V	Fermor <i>et al.</i> (1979); Corominas <i>et al.</i> (1987); Strauch (1987); Hardy and Sivisithamparam (1989); Beffa <i>et al.</i> (1996b); Masanori and Kazuo (1998); Tuitert <i>et al.</i> (1998); Mannix <i>et al.</i> (2001)
<i>Pseudomonas stutzeri</i>	m, t	A, M, O	Hoitink and Fahy (1986); Andrews <i>et al.</i> (1994); Koschinsky <i>et al.</i> (1998)
<i>Pseudonocardia asaccharolytica</i> °	m	M	Reichert <i>et al.</i> (1998)
<i>Pseudonocardia sp.</i> °	t	P	Henssen (1957)
<i>Pseudonocardia sulfidoxydans</i> °	m	M	Reichert <i>et al.</i> (1998)
<i>Pseudonocardia thermophila</i> °	t	O	Fergus (1964)
<i>Psychrobacter immobilis</i>	m	A	Andrews <i>et al.</i> (1994)
<i>Rathayibacter tritici</i> °	m	A	J. Mergaert, unpublished data
<i>Rhodococcus rhodochrous</i> °	m	A, G	Ryckeboer <i>et al.</i> (2003); J. Ryckeboer, unpublished data
<i>Rhodococcus sp.</i>	m	Y	Rocha <i>et al.</i> (2002)
<i>Rhodovulum adriaticum</i>	m	A	J. Mergaert, unpublished data
<i>Saccharomonospora sp.</i> °	t	O	Amner <i>et al.</i> (1988)
<i>Serratia entomophila</i>	m	A	Andrews <i>et al.</i> (1994)
<i>Serratia marcescens</i>	m	A, U	Andrews <i>et al.</i> (1994); Droffner <i>et al.</i> (1995)
<i>Serratia sp.</i>	m	O, U	Fermor <i>et al.</i> (1979), Strauch (1987)

(continued)

TABLE 3 – Overview of prokaryotes reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Sphingobacterium thalophilum</i>	m	P	Kaneshiro <i>et al.</i> (1995)
<i>Staphylococcus intermedius</i>	t	A	Ryckeboer <i>et al.</i> (2003)
<i>Staphylococcus</i> sp.	m	P, U	Kaneshiro <i>et al.</i> (1995); Mannix <i>et al.</i> (2001)
<i>Stenotrophomonas maltophilia</i> (syn.: <i>Xanthomonas maltophilia</i>)	m	A, M	Hoitink and Fahy (1986); Hoitink (1990); Andrews <i>et al.</i> (1994)
<i>Streptomyces fradiae</i> °	t	K	Corbaz <i>et al.</i> (1963)
<i>Streptomyces griseoflavus</i> °	t	K	Corbaz <i>et al.</i> (1963)
“ <i>Streptomyces rectus</i> ” °	m, t	O	Fergus (1964)
<i>Streptomyces</i> sp. °	m, t	A, D, O, U	Henssen (1957); Golueke (1977); Fermor <i>et al.</i> (1979); Strom (1985b); Strauch (1987); Amner <i>et al.</i> (1988); Mergaert <i>et al.</i> (1994a); Mergaert and Swings (1996); Breitenbach (1998); Ryckeboer <i>et al.</i> (2003)
<i>Streptomyces thermoviolaceus</i> °	t	B, O	Fergus (1969); Gangwar <i>et al.</i> (1997)
<i>Streptomyces thermoviolaceus</i> subsp. <i>apingens</i> °	t	K, O	Corbaz <i>et al.</i> (1963); Fergus (1964)
<i>Streptomyces thermovulgaris</i> °	t	O	Fergus (1964); Fermor <i>et al.</i> (1979)
<i>Streptomyces violaceoruber</i> °	m, t	O	Fergus (1964)
<i>Symbiobacterium</i> sp.	t	U	Ueda <i>et al.</i> (2002)
<i>Symbiobacterium thermophilum</i>	t	U	Ohno <i>et al.</i> (2000)
<i>Terrabacter</i> sp.	m	Y	Rocha <i>et al.</i> (2002)
“ <i>Thermoactinomyces glaucus</i> ” °	m, t	O	Fergus (1964)
<i>Thermoactinomyces</i> sp. °	t	D, O, P	Henssen (1957); Atrom (1985a, 1985b); Amner <i>et al.</i> (1988)
<i>Thermoactinomyces vulgaris</i> °	m, t	O	Fergus (1964); Fermor <i>et al.</i> (1979)
<i>Thermobifida fusca</i> (syn.: <i>Thermomonospora fusca</i>) °	m, t	G, O	Fergus (1964); Kleeberg <i>et al.</i> (1998)
<i>Thermocrispum agreste</i>	m, t	O	Korn-Wendisch <i>et al.</i> (1995)
<i>Thermocrispum municipale</i>	m, t	B	Korn-Wendisch <i>et al.</i> (1995)
<i>Thermocrispum</i> sp.	m, t	B	Korn-Wendisch <i>et al.</i> (1995)
<i>Thermomonospora curvata</i> °	m, t	B, O	Fergus (1964); Gangwar <i>et al.</i> (1997)

(continued)

TABLE 3 – Overview of prokaryotes reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Thermomonospora</i> sp. °	t	O, P	Henssen (1957); Amner <i>et al.</i> (1988)
“ <i>Thermomonospora viridis</i> ” °	t	O	Fermor <i>et al.</i> (1979)
“ <i>Thermopolyspora polyspora</i> ”	t	K, O	Corbaz <i>et al.</i> (1963); Fergus (1964)
“ <i>Thermopolyspora glauca</i> ”	t	K	Corbaz <i>et al.</i> (1963)
“ <i>Thermopolyspora</i> ” sp.	t	P	Henssen (1957)
<i>Thermus</i> sp.	t	A, W	Fujio and Kume (1991); Beffa <i>et al.</i> (1996b, 1996c)
<i>Thermus thermophilus</i>	t	A	Blanc <i>et al.</i> (1998)
<i>Variovorax paradoxus</i>	m	U	Mergaert <i>et al.</i> (1994a); Mergaert and Swings (1996)
<i>Xanthobacter</i> sp.	m	A, Y	Beffa <i>et al.</i> (1996b); Rocha <i>et al.</i> (2002)

The majority of the species presented in this table were isolated on rich organic complex media.

* The most recent names are given. When older synonyms were cited in the referenced literature, these are given in parenthesis. Species names between brackets have not been listed on the Approved Names of Bacterial Names (Skerman *et al.*, 1980) or have not been subsequently validly published or validated. Taxa (or their older synonyms) assigned to the actinomycetes by Goodfellow (1989) are marked with °.

** Temperature phase: m = mesophilic; t = thermophilic; prokaryotes are classified as mesophiles and thermophiles if their optimal growth temperatures are moderate (20-40 °C) or high (> 40 °C); respectively.

*** Source material: A = kitchen and garden waste (= vegetable, fruit and garden waste; leaves, grass and food waste; source-separated household waste); B = municipal solid waste; C = food waste and sawdust; D = kitchen waste and shredded newspapers; F = grass compost; G = garden waste; I = compost of manure, grass and rice straw; K = moldy hay; M = hardwood bark; tree bark; eucalyptus bark; N = peanut shells; O = mushroom compost; P = horse manure; dairy cattle manure; manure (several origins); Q = poultry litter; R = sludge, barks (chicken manure and wood chips) and garbage; U = compost (origin not defined); V = agricultural waste; W = sewage sludge; Y = cattle manure and forestry wastes.

Thermophilic phase

As soon as moisture decreases, temperature rises above 30 °C and the substrates become more alkaline, actinomycetes, in particular streptomycetes, thrive. They cause the characteristic earthy smell of soil and compost by production of geosmine, which are sesquiterpenoid compounds. Actinomycetes compete with other organisms for nutrients and can inhibit microbial growth by production of antibiotics, lytic enzymes or even by parasitism. They play an important role in composting by degrading natural polymers and colonize organic material after bacteria and fungi have consumed easily degradable fractions. Their enzymes enable

TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Absidia corymbifera</i> (Cohn) Saccardo & A. Trotter 1912 (syn.: <i>Mucor corymbifer</i> Cohn 1884)	m, t	B, J, O, G	Von Klopotek (1962); Chang and Hudson (1967); Knoesel and Resz (1973); Upreti and Joshi (1984); Anastasi <i>et al.</i> (2002)
<i>Absidia orchidis</i> Vuillemin 1908	m	O	Upreti and Joshi (1984)
<i>Absidia ramosa</i> (Lindt) Lendner 1908	t	E, O	de Bertoldi <i>et al.</i> (1983); Upreti and Joshi (1984)
<i>Absidia</i> sp.	m	B	Von Klopotek (1962)
<i>Acremoniella</i> sp.	t	H	Waksman <i>et al.</i> (1939a)
<i>Acremonium atrogriseum</i> (Panasenko) W. Gams 1971	m	A	Breitenbach (1998)
<i>Acremonium breve</i> (Sukapure & Thirumalachar) W. Gams 1971		X	Anastasi <i>et al.</i> (2002)
<i>Acremonium butyri</i> (van Beyma) W. Gams 1971		O	Fagan and Fergus (1984)
<i>Acremonium charticola</i> (Lindau) W. Gams 1971		G	Anastasi <i>et al.</i> (2002)
<i>Acremonium chrysogenum</i> (Thirumalachar & Sukapure) W. Gams 1971	m	A, G, X	Breitenbach (1998), Anastasi <i>et al.</i> (2002)
<i>Acremonium furcatum</i> 1970 (F. & V. Moreau) ex W. Gams	m	A	J. Ryckeboer, unpublished data
<i>Acremonium kiliense</i> Grütz 1925 (syn.: <i>Cephalosporium kiliense</i> (Grütz) Hartmann)	m	A	Breitenbach (1998); J. Ryckeboer, unpublished data
<i>Acremonium murorum</i> (Corda) W. Gams 1971 (syn.: <i>Gliomastix murorum</i> (Corda) S. Hughes 1958)	m	E	de Bertoldi <i>et al.</i> (1983)
<i>Acremonium sclerotigenum</i> (F. & V. Moreau ex Valenta) W. Gams 1971		G, X	Anastasi <i>et al.</i> (2002)
<i>Acremonium</i> sp.	m	A, G, O, X	Fagan and Fergus (1984); Breitenbach (1998); Anastasi <i>et al.</i> (2002); Ryckeboer <i>et al.</i> (2003)
<i>Acremonium strictum</i> W. Gams 1971	m	A, G, H, X	Eastwood (1952); Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Acremonium thermophilum</i> W. Gams & Lacey 1972	m, t	A	J. Ryckeboer, unpublished data

(continued)

TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Acremonium verruculosum</i> W. Gams & Veenbaas-Rijks 1971		X	Anastasi <i>et al.</i> (2002)
<i>Acrodontium griseum</i> (Fassatiová) de Hoog 1972		G	Anastasi <i>et al.</i> (2002)
<i>Acrophialophora fusispora</i> (S.B. Saksena) Samson 1970		G, X	Anastasi <i>et al.</i> (2002)
<i>Actinomucor elegans</i> (Eidam) C.R. Benjamin & Hesseltine 1957 (syn.: <i>A. repens</i> Schotstakowitsch. 1898)	m	A, G	Domsch (1960b); Von Klopotek (1962); Breitenbach (1998)
<i>Actinomucor</i> sp.	m	B	Von Klopotek (1962)
<i>Agaricus bisporus</i> (J. Lange) Imbach (syn.: <i>Agaricus</i> <i>brunnescens</i> Peck)		O	Fagan and Fergus (1984)
<i>Aleurisma</i> sp.	m	B	Von Klopotek (1962)
<i>Alternaria alternata</i> (Fries: Fries) von Keissler 1912 (syn.: <i>A. tenuis</i> Nees 1822)	m	A, B, E, F, G, J, X	Eastwood (1952); Von Klopotek (1962); Chang and Hudson (1967); de Bertoldi <i>et al.</i> (1983); Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Alternaria</i> sp.	m	P, Y	Waksman <i>et al.</i> (1939a); Rocha <i>et al.</i> (2002)
<i>Aphanoascus terreus</i> (Randhawa & Sandhu) Apinis		X	Anastasi <i>et al.</i> (2002)
<i>Apiospora montagnei</i> Saccardo 1875		X	Anastasi <i>et al.</i> (2002)
<i>Armillaria mellea</i> (Vahl: Fries) P. Kummer 1871		E	de Bertoldi <i>et al.</i> (1983)
<i>Arthrimum phaeospermum</i> (Corda) M.B. Ellis 1965		G	Domsch (1960a)
<i>Arthrobotrys amerospora</i> S. Schenck <i>et al.</i> 1976	m	A	Breitenbach (1998)
<i>Arthrobotrys oligospora</i> Fresenius 1850	m	A, E, G, O	de Bertoldi <i>et al.</i> (1983); Fagan and Fergus (1984); Domsch <i>et al.</i> (1993); Breitenbach (1998)
<i>Arthrobotrys</i> sp.	m	B, G	Von Klopotek (1962); Chamuris <i>et al.</i> (2000)
<i>Ascodesmis microscopica</i> (Crouan) Seaver		G	Anastasi <i>et al.</i> (2002)

(continued)

TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Ascotricha</i> sp.	m	B	Von Klopotek (1962)
<i>Aspergillus candidus</i> Link: Fries	m	A, G, J, X	Domsch (1960a); Chang and Hudson (1967); Anastasi <i>et al.</i> (2002); Ryckeboer <i>et al.</i> (2003); J. Ryckeboer, unpublished data
<i>Aspergillus clavatus</i> Desmazières 1834	m	B	Von Klopotek (1962)
<i>Aspergillus erythrocephalus</i> Berk. & Curtis 1869	m	F	Malik and Sandhu (1973)
<i>Aspergillus flavipes</i> (Bain. & Sart) Thom & Church	m	O	Upreti and Joshi (1984)
<i>Aspergillus flavus</i> Link 1821	m	O	Upreti and Joshi (1984)
<i>Aspergillus flavus</i> var. <i>columnaris</i> Raper & Fennell 1965		G, X	Anastasi <i>et al.</i> (2002)
<i>Aspergillus flavus</i> var. <i>flavus</i> Link: Fries 1809		G	Anastasi <i>et al.</i> (2002)
<i>Aspergillus fumigatus</i> Fresenius 1863	m, t	A, B, D, E, F, J, L, M, O, U	Eastwood (1952); Von Klopotek (1962); Fergus (1964); Chang and Hudson (1967); Stutzenberger <i>et al.</i> (1970); Knoesel and Resz (1973); Malik and Sandhu (1973); Golueke (1977); Fermor <i>et al.</i> (1979); de Bertoldi <i>et al.</i> (1983); Upreti and Joshi (1984); Strom (1985b); Campbell <i>et al.</i> (1990); Mergaert <i>et al.</i> (1994a); Beffa <i>et al.</i> (1996b); Lott Fischer (1996); Mergaert and Swings (1996); Breitenbach (1998); Chamuris <i>et al.</i> (2000)
<i>Aspergillus fumigatus</i> var. <i>ellipticus</i> Raper & Fennell 1965	m	A, G, X	Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Aspergillus fumigatus</i> var. <i>fumigatus</i> Fresenius 1863	m	A, G, X	Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Aspergillus melleus</i> Yukawa 1911 (syn.: <i>Aspergillus quercinus</i> (Bainier) Thom & Church 1926)	m	B	Von Klopotek (1962)
<i>Aspergillus nidulans</i> (Eidam) G. Winter 1884	m	A	Breitenbach (1998)

(continued)

TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Aspergillus niger</i> van Tieghem 1867	m	B, F, G, O, X	Von Klopotek (1962); Malik and Sandhu (1973); Upreti and Joshi (1984); Chamuris <i>et al.</i> (2000); Anastasi <i>et al.</i> (2002)
<i>Aspergillus ochraceous</i> Wilhelm 1877	m	G, O, X	Upreti and Joshi (1984); Anastasi <i>et al.</i> (2002)
<i>Aspergillus oryzae</i> var. <i>oryzae</i> (Ahlburg) Cohn		G	Anastasi <i>et al.</i> (2002)
<i>Aspergillus parasiticus</i> Speare 1912	m	O	Upreti and Joshi (1984)
<i>Aspergillus puniceus</i> Kwon & Fennell 1965		X	Anastasi <i>et al.</i> (2002)
<i>Aspergillus ruber</i> (Kon. Spieck. & Bremer) Thom & Church 1926	m	O	Upreti and Joshi (1984)
<i>Aspergillus</i> sp.	m, t	A, B, E, F, G, M, N, P, X, Y	Eastwood (1952); Henssen (1957); Von Klopotek (1962); de Bertoldi <i>et al.</i> (1983); Chung and Hoitink (1990); Seck and Kilbertus (1996); Breitenbach (1998); Anastasi <i>et al.</i> (2002); Rocha <i>et al.</i> (2002); Ryckeboer <i>et al.</i> (2003); J. Ryckeboer, unpublished data
<i>Aspergillus sulphureus</i> (Fresenius) Thom & Church		X	Anastasi <i>et al.</i> (2002)
<i>Aspergillus sydowii</i> (Bain. & Sart) Thom & Church 1926	m	O	Upreti and Joshi (1984)
<i>Aspergillus terreus</i> Thom 1918	m, t	F, J, O	Eastwood (1952); Upreti and Joshi (1984)
<i>Aspergillus terreus</i> var. <i>africanus</i> Fennell & Raper 1955		G	Anastasi <i>et al.</i> (2002)
<i>Aspergillus terreus</i> var. <i>terreus</i> Thom		G, X	Anastasi <i>et al.</i> (2002)
<i>Aspergillus versicolor</i> (Vuillemin) Tiraboschi 1926	m	A, D, G, M	Domsch (1960b); Chang and Hudson (1967); Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Aspergillus wentii</i> Wehmer 1896		G	Anastasi <i>et al.</i> (2002)
<i>Aureobasidium pullulans</i> (de Bary) Arnaud 1910	m	F, G, O	Malik and Sandhu (1973); Fermor <i>et al.</i> (1979); Chamuris <i>et al.</i> (2000)

(continued)

TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Aureobasidium pullulans</i> var. <i>pullulans</i> (de Bary) Arnaud		X	Anastasi <i>et al.</i> (2002)
<i>Aureobasidium</i> sp.	m	J	Chang and Hudson (1967)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin 1912		X	Anastasi <i>et al.</i> (2002)
<i>Beauveria brongniartii</i> (Saccardo) Petch 1926		X	Anastasi <i>et al.</i> (2002)
<i>Beauveria felina</i> (de Candolle: Fries) Carmichael 1980 (syn.: <i>Isaria cretacea</i> van Beyma)	m	B	Von Klopotek (1962)
<i>Botryosporium</i> sp.		U	Golueke (1977)
<i>Botryotinia fuckeliana</i> (de Bary) Whetzel 1945 (alternative state of <i>Botrytis cinerea</i> Persoon: Fries)		X	Anastasi <i>et al.</i> (2002)
<i>Botryotrichum piluliferum</i> Sacc. & March. 1885	m	A, E, O	de Bertoldi <i>et al.</i> (1983); Fagan and Fergus (1984); Breitenbach (1998)
<i>Botryotrichum</i> sp.		O	Fagan and Fergus (1984)
<i>Botrytis cinerea</i> Persoon Ex Nocca & Balb. 1822	m	A, G, O	Fermor <i>et al.</i> (1979); Breitenbach (1998); Chamuris <i>et al.</i> (2000)
<i>Botrytis</i> sp.	m	B	Von Klopotek (1962)
<i>Candida krusei</i> (Castellani) Berkhout 1923 (alternate state of <i>Issatchenkia orientalis</i> Kudrjanzev 1960)		Z	Peters <i>et al.</i> (2000)
<i>Candida tropicalis</i> (Castellani) Berkhout 1923		Z	Peters <i>et al.</i> (2000)
<i>Cephalophora irregularis</i> Thaxter 1903	m	B	Von Klopotek (1962)
<i>Cephalophora</i> sp.	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Cephalophora tropica</i> Thaxter 1903	m	B, E	Von Klopotek (1962); de Bertoldi <i>et al.</i> (1983)
<i>Cephalosporium</i> sp.	m	A, B, E, G, H, O, P	Waksman <i>et al.</i> (1939a); Eastwood (1952); Von Klopotek (1962); Fermor <i>et al.</i> (1979); de Bertoldi <i>et al.</i> (1983); J. Ryckeboer, unpublished data

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Chaetomidium fimeti</i> (Fuckel) Saccardo 1882 (syn.: <i>Thielavia fimeti</i> (Fuckel) Malloch & Cain 1973)		G	Domsch (1960b)
<i>Chaetomium bostrychodes</i> Zopf 1877		X	Anastasi <i>et al.</i> (2002)
<i>Chaetomium funicola</i> Cooke 1873 (syn.: <i>Chaetomium dolichotrichum</i> L. Ames 1945)	m	B, X	Von Klopotek (1962); Anastasi <i>et al.</i> (2002)
<i>Chaetomium globosum</i> Kunze: Fries	m	F, J, X	Eastwood (1952); Malik and Sandhu (1973); Anastasi <i>et al.</i> (2002)
<i>Chaetomium indicum</i> Corda 1840	m	B	Von Klopotek (1962)
<i>Chaetomium nigricolor</i> L. Ames 1950		G	Anastasi <i>et al.</i> (2002)
<i>Chaetomium olivaceum</i> Cooke & Ellis 1878	m	O	Botha <i>et al.</i> (1990)
<i>Chaetomium</i> sp.	m	E, G, Y	de Bertoldi <i>et al.</i> (1983); Chamuris <i>et al.</i> (2000), Rocha <i>et al.</i> (2002)
<i>Chaetomium thermophile</i> var. <i>coprophile</i> Cooney & Emerson 1964	t	O	Upreti and Joshi (1984)
<i>Chaetomium thermophile</i> var. <i>dissetum</i> Cooney & Emerson 1964	t	O	Upreti and Joshi (1984)
<i>Chaetomium thermophilum</i> La Touche 1950	t	B, E, J, O, U	Von Klopotek (1962); Fergus (1964); Chang and Hudson (1967); Fergus (1969); Kane and Mullins (1973); Golueke (1977); Fermor <i>et al.</i> (1979); de Bertoldi <i>et al.</i> (1983)
<i>Chrysosporium indicum</i> (Randhawa & Sandhu) Garg 1965		X	Anastasi <i>et al.</i> (2002)
<i>Chrysosporium merdarium</i> (Link: Fries) Carmichael 1962		X	Anastasi <i>et al.</i> (2002)
<i>Chrysosporium queenslandicum</i> Apinis & Rees 1976		X	Anastasi <i>et al.</i> (2002)
<i>Chrysosporium tropicum</i> Carmichael 1962		X	Anastasi <i>et al.</i> (2002)
<i>Circinella umbellata</i> van Tieghem & le Monnier 1873	m	B	Von Klopotek (1962)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Cladosporium chlorocephalum</i> (Fresenius) Mason & M.B. Ellis		G	Anastasi <i>et al.</i> (2002)
<i>Cladosporium cladosporioides</i> (Fresenius) de Vries 1952	m	A, B, G, O, X	Von Klopotek (1962); Upreti and Joshi (1984); Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Cladosporium herbarum</i> (Persoon: Fries) Link 1821	m	A, G, J, O, X	Chang and Hudson (1967); Fermor <i>et al.</i> (1979); Breitenbach (1998); Anastasi <i>et al.</i> (2002); J. Ryckeboer, unpublished data
<i>Cladosporium oxysporum</i> Berkeley & Curtis 1868		G, X	Anastasi <i>et al.</i> (2002)
<i>Cladosporium</i> sp.	m	B, Y	Von Klopotek (1962); Rocha <i>et al.</i> (2002)
<i>Cladosporium sphaerospermum</i> Penzig 1882		G, X	Anastasi <i>et al.</i> (2002)
<i>Clitopilus pinsitus</i> (Fries) Jossierand	m	J	Chang and Hudson (1967)
<i>Clonostachys rosea</i> (Link: Fries) Schroers, Samuels, Seifert & W. Gams 1999	m	A	Breitenbach (1998)
<i>Clonostachys solani</i> (Harting) Schroers & W. Gams	m	A	Breitenbach (1998)
<i>Coniothyrium fuckelii</i> Saccardo 1878		G, X	Anastasi <i>et al.</i> (2002)
<i>Coniothyrium sporulosum</i> (W. Gams & Domsch) van der Aa 1977		G	Domsch (1960b)
<i>Coonemeria crustacea</i> (Apinis & Chesters) Mouch. 1997 (syn.: <i>Dactylomyces crustaceus</i> Apinis & Chesters 1964)	t	B	Kane and Mullins (1973)
<i>Coprinus cinereus</i> (Schaeffer: Fries) Gray 1928 (syn.: <i>Coprinus delicatulus</i> Apinis 1965)	m, t	E, J, O	Chang and Hudson (1967); de Bertoldi <i>et al.</i> (1983); Fagan and Fergus (1984); Straatsma <i>et al.</i> (1994); Tuomela <i>et al.</i> (2000)
<i>Coprinus congregatus</i> (Bulliard) Fries		O	Fagan and Fergus (1984)
<i>Coprinus domesticus</i> (Bolton: Fries) Gray 1821		O	Fagan and Fergus (1984)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Coprinus</i> sp.	m	B, J, O	Von Klopotek (1962); Chang and Hudson (1967); Fagan and Fergus (1984)
<i>Corynascus sepedonium</i> (C.W. Emmons) von Arx 1973 (syn.: <i>Thielavia sepedonium</i> Emmons 1932)	m	G, O, X	Fagan and Fergus (1984); Chamuris <i>et al.</i> (2000); Anastasi <i>et al.</i> (2002)
<i>Cunninghamella elegans</i> Lendner 1908		X	Anastasi <i>et al.</i> (2002)
<i>Curvularia harveyi</i> Shipton 1966	m	G	Chamuris <i>et al.</i> (2000)
<i>Curvularia pallescens</i> Boedijn 1933	m	O	Upreti and Joshi (1984)
<i>Cylindrocarpon destructans</i> (Zinssmeister) Scholten 1964	m	G	Chamuris <i>et al.</i> (2000)
<i>Cylindrocarpon lichenicola</i> (C.B. Massalongo) Hawksworth 1979 (syn.: <i>C. tonkinense</i> Bugnicourt 1939)	m	A	Breitenbach (1998)
<i>Cylindrocarpon</i> sp.	m	G	Chamuris <i>et al.</i> (2000); Anastasi <i>et al.</i> (2002)
<i>Dactylaria</i> sp.	m	A	Ryckeboer <i>et al.</i> (2003)
<i>Doratomyces medius</i> (Sacc.) Matsush. 1980	m	A	Breitenbach (1998)
<i>Doratomyces microsporus</i> (Saccardo) Morton & Smith 1963		G, O, P	Domsch (1960b); Fagan and Fergus (1984); Domsch <i>et al.</i> (1993); Anastasi <i>et al.</i> (2002)
<i>Doratomyces purpureofuscus</i> (Schweinitz: Fries) Morton & Smith 1963		B, O, X	Morton and Smith (1963); Fagan and Fergus (1984); Domsch <i>et al.</i> (1993); Anastasi <i>et al.</i> (2002)
<i>Doratomyces</i> sp.	m	E	de Bertoldi <i>et al.</i> (1983)
<i>Doratomyces stemonitis</i> (Persoon: Fries) Morton & G. Smith 1963 (syn.: <i>Stysanus stemonitis</i> (Persoon: Fries) Corda 1837)	m	A, B, G, J	Domsch (1960b); Von Klopotek (1962); Chang and Hudson (1967); Breitenbach (1998)
<i>Emericella nidulans</i> (Eidam) Vuillemin 1927 (anamorph: <i>Aspergillus nidulans</i> (Eidam) Winter 1884)	m, t	E, G, J, O	Domsch (1960a); Chang and Hudson (1967); de Bertoldi <i>et al.</i> (1983); Upreti and Joshi (1984); Chamuris <i>et al.</i> (2000)
<i>Emericella nidulans</i> var. <i>nidulans</i> (Eidam) Vuillemin		X	Anastasi <i>et al.</i> (2002)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Emericella quadrilineata</i> (Thom & Raper) C.R. Benjamin 1955 (anamorph: <i>Aspergillus quadrilineatus</i> Thom & Raper 1939)	m	B	Von Klopotek (1962)
<i>Engyodontium album</i> (Limber) de Hoog 1972		X	Anastasi <i>et al.</i> (2002)
<i>Epicoccum nigrum</i> Link ex Link 1825 (syn.: <i>E. purpurascens</i> Ehrenberg ex Schlecht 1824)	m	A, B, G, X	Domsch (1960b); Von Klopotek (1962); Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Eremascus fertilis</i> Stoppel 1907		G	Anastasi <i>et al.</i> (2002)
<i>Eurotium amstelodami</i> Mangin 1909 (syn.: <i>Aspergillus amstelodami</i> (Mangin) Thom & Church 1926)	m	E, G, J, X	Chang and Hudson (1967); de Bertoldi <i>et al.</i> (1983); Anastasi <i>et al.</i> (2002)
<i>Eurotium chevalieri</i> Mangin 1909		X	Anastasi <i>et al.</i> (2002)
<i>Eurotium herbariorum</i> (Wiggers: Fries) Link ex Gray 1821 (syn.: <i>E. repens</i> de Bary 1870; anamorph: <i>Aspergillus repens</i> (Corda) Saccardo 1882)	m	G, J	Domsch (1960a); Chang and Hudson (1967)
<i>Eurotium intermedium</i> Blaser 1975		X	Anastasi <i>et al.</i> (2002)
<i>Eurotium montevidense</i> (Talice & Mackinnon) Malloch & Cain 1972		G	Anastasi <i>et al.</i> (2002)
<i>Eurotium rubrum</i> König <i>et al.</i>		X	Anastasi <i>et al.</i> (2002)
<i>Eutypella scoparia</i> (Schweinitz: Fries) Ellis & Everhart 1892		G	Anastasi <i>et al.</i> (2002)
<i>Exophiala moniliae</i> de Hoog 1977		G	Anastasi <i>et al.</i> (2002)
<i>Exophiala pisciphila</i> McGinnis & Ajello 1974		X	Anastasi <i>et al.</i> (2002)
<i>Exophiala</i> sp.		X	Anastasi <i>et al.</i> (2002)
<i>Fennellia nivea</i> (Wiley & Simmons) Samson		X	Anastasi <i>et al.</i> (2002)
<i>Fomes</i> sp.	t	E	de Bertoldi <i>et al.</i> (1983)
<i>Fusarium culmorum</i> (W.G. Smith) Saccardo 1895	m	A, J	Chang and Hudson (1967); Breitenbach (1998)
<i>Fusarium dimerum</i> Penzig 1882		G	Domsch (1960a)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Fusarium filiferum</i> (Preuss) Wollenw 1916	m	A	Breitenbach (1998)
<i>Fusarium merismoides</i> Corda Domsch (1960b) 8		G	Domsch (1960a)
<i>Fusarium oxysporum</i> Schlechtendahl: Fries 1824	m	G	Chamuris <i>et al.</i> (2000); Anastasi <i>et al.</i> (2002)
<i>Fusarium solani</i> (Martius) Saccardo 1881	m	A, F, G, O	Malik and Sandhu (1973); Fagan and Fergus (1984); Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Fusarium</i> sp.	m	A, B, G, H, N, O, S, X	Eastwood (1952); Von Klopotek (1962); Fagan and Fergus (1984); Hadar and Gorodecki (1991); Seck and Kilbertus (1996); Breitenbach (1998); Chamuris <i>et al.</i> (2000); Anastasi <i>et al.</i> (2002); J. Ryckeboer, unpublished data
<i>Fusarium verticillioides</i> (Saccardo) Nirenberg 1976 (syn.: <i>Fusarium moniliforme</i> Sheldon 1904)	m	O	Upreti and Joshi (1984)
<i>Gelasinospora reticulata</i> (Booth & Ebben) Cailleux 1972 (syn.: <i>Anixiella reticulata</i> (Booth & Ebben) Cain 1961)		O	Fagan and Fergus (1984)
<i>Geomyces pannorum</i> (Link) Sigler & Carmichael 1976	m	A	Breitenbach (1998)
<i>Geomyces pannorum</i> var. <i>pannorum</i> (Link) Sigler & Carmichael 1976		G, X	Anastasi <i>et al.</i> (2002)
<i>Geomyces vinaceus</i> Dal Vesco 1957		G	Anastasi <i>et al.</i> (2002)
<i>Geosmithia</i> sp.	t	M	Campbell <i>et al.</i> (1990)
<i>Geotrichum candidum</i> Link ex Leman 1821	m	A, B, E, U	Von Klopotek (1962); de Bertoldi <i>et al.</i> (1983); Strauch and de Bertoldi (1985); Breitenbach (1998); Ryckeboer <i>et al.</i> (2003); J. Ryckeboer, unpublished data
<i>Geotrichum</i> sp.	m	G, O, X, Y	Fagan and Fergus (1984); Chamuris <i>et al.</i> (2000); Anastasi <i>et al.</i> (2002); Rocha <i>et al.</i> (2002)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Gilmaniella humicola</i> Barron 1964	m	G, O	Bollen and Van der Pol-Luiten (1975); Fagan and Fergus (1984); Chamuris <i>et al.</i> (2000)
<i>Gilmaniella macrospora</i> Moustafa 1975		X	Anastasi <i>et al.</i> (2002)
<i>Gliobotryx alboviridis</i> von Höhnell	m	B	Von Klopotek (1962)
<i>Gliocladium deliquescens</i> Sopp.	m	O	Upreti and Joshi (1984)
<i>Gliocladium penicillioides</i> Corda 1870	m	F	Eastwood (1952)
<i>Gliocladium roseum</i> Bainier 1907	m	A, B	Von Klopotek (1962); Ryckeboer <i>et al.</i> (2003)
<i>Gliocladium</i> sp.	m	E, G	de Bertoldi <i>et al.</i> (1983); Anastasi <i>et al.</i> (2002)
<i>Gliocladium viride</i> Matruchot 1893	m	B	Von Klopotek (1962)
<i>Gliomastix</i> cf. <i>atrogriseum</i> (Panas.) Borowska 1986	m	A	Breitenbach (1998)
<i>Gliomastix</i> sp.	m	B	Von Klopotek (1962)
<i>Gloeophyllum trabeum</i> (Persoon: Fries) Murril 1908 (syn.: <i>Lenzites trabea</i> (Persoon) Bres. 1897)	m	E	de Bertoldi <i>et al.</i> (1983)
<i>Graphium putredinis</i> (Corda) S. Hughes 1958	m	A, X	Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Graphium</i> sp.	m	B	Von Klopotek (1962)
<i>Gymnoascaceae</i> sp.		G	Anastasi <i>et al.</i> (2002)
<i>Harpographium</i> sp.	m	E	de Bertoldi <i>et al.</i> (1983)
<i>Heterosporium</i> sp.	m	B	Von Klopotek (1962)
<i>Hormiscium</i> sp.	m, t	B	Von Klopotek (1962)
<i>Humicola fuscoatra</i> Traaen 1914	m	A	Breitenbach (1998)
<i>Humicola fuscoatra</i> var. <i>fuscoatra</i> Traaen 1914		G, X	Anastasi <i>et al.</i> (2002)
<i>Humicola grisea</i> ^d Traaen	m, t	B, O	Von Klopotek (1962); Fergus (1969); Fermor <i>et al.</i> (1979); Campbell <i>et al.</i> (1990)
<i>Humicola grisea</i> var. <i>thermoidea</i> ^a Cooney & Emerson 1964	t	O, X	Fergus (1964); Fermor <i>et al.</i> (1979); Upreti and Joshi (1984); Anastasi <i>et al.</i> (2002)
<i>Humicola insolens</i> ^a Cooney & Emerson 1964	m, t	E, J, O	Fergus (1964); Chang and Hudson (1967); Fergus (1969); de Bertoldi <i>et al.</i> (1983); Upreti and Joshi (1984)

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Organism*	Temperature phase**	Source material***	Reference
<i>Humicola</i> sp.	t	A, B, M, P	Waksman <i>et al.</i> (1939a); Henssen (1957); Von Klopotek (1962); Chung and Hoitink (1990); J. Ryckeboer, unpublished data
<i>Hypocrea lutea</i> (Tode) Petch 1937 (syn.: <i>Gliocladium deliquescens</i> Olsen-Sopp)	m	B	Von Klopotek (1962)
<i>Hypomyces chrysospermus</i> (Bulliard) Tulasne 1860		G	Domsch (1960a)
<i>Kluyveromyces marxianus</i> (E.C. Hansen) Van der Walt 1965	m, t	C	Choi and Park (1998)
<i>Lentinus lepideus</i> (Fries: Fries) Fries 1838	m	E	de Bertoldi <i>et al.</i> (1983)
<i>Lenzites</i> sp.	t	E	de Bertoldi <i>et al.</i> (1983)
<i>Leptographium lundbergii</i> Lagerberg & Melin	m	E	de Bertoldi <i>et al.</i> (1983)
<i>Leptographium</i> sp.		G, X	Anastasi <i>et al.</i> (2002)
<i>Macrosporium</i> sp.	m	B	Von Klopotek (1962)
<i>Malbranchea cinnamomea</i> (Libert) van Oorschot & de Hoog 1984 (syn.: <i>Malbranchea pulchella</i> (Miehe) Sigler & Carmichael 1976; <i>Thermoidium sulfureum</i> Miehe)	t	B, G, J, O, X	Von Klopotek (1962); Chang and Hudson (1967); Fergus (1969); Straatsma <i>et al.</i> (1994); Anastasi <i>et al.</i> (2002)
<i>Melanocarpus albomyces</i> (Cooney & Emerson) von Arx 1975 (syn.: <i>Myriococcum albomyces</i> Cooney & Emerson 1964)		O, U	Tuomela <i>et al.</i> (2000)
<i>Metarhizium flavoviride</i> W. Gams & Rozsypal 1973	m	A	J. Ryckeboer, unpublished data
<i>Microascus cirrosus</i> Curzi 1930		X	Anastasi <i>et al.</i> (2002)
<i>Mollisia</i> sp.	t	E	de Bertoldi <i>et al.</i> (1983)
<i>Monilia</i> sp.	m, t	A, O, P	Waksman <i>et al.</i> (1939a); Fermor <i>et al.</i> (1979); Breitenbach (1998)
<i>Moniliella suaveolens</i> var. <i>nigra</i> (Burri & Staub) de Hoog 1979		X	Anastasi <i>et al.</i> (2002)
<i>Monotospora</i> sp.	t	H, P	Waksman <i>et al.</i> (1939a); Eastwood (1952)
<i>Mortierella alliacea</i> Linnemann 1953		G	Anastasi <i>et al.</i> (2002)

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Organism*	Temperature phase**	Source material***	Reference
<i>Mortierella alpina</i> Peyronel 1913		G, X	Anastasi <i>et al.</i> (2002)
<i>Mortierella chlamydospora</i> (Chesters) van der Plaats-Niterink 1976		G	Anastasi <i>et al.</i> (2002)
<i>Mortierella echinosphaera</i> van der Plaats-Niterink 1976		G, X	Anastasi <i>et al.</i> (2002)
<i>Mortierella exigua</i> Linnemann 1941		G	Domsch (1960b)
<i>Mortierella globalpina</i> W. Gams & Veenbaas-Rijks 1976		G	Anastasi <i>et al.</i> (2002)
<i>Mortierella humilis</i> Linnemann ex W. Gams 1977		G	Anastasi <i>et al.</i> (2002)
<i>Mortierella hyalina</i> (Harz) W. Gams 1969 (syn.: <i>Mortierella hygrophila</i> Linnemann 1936)	m	A, G	Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Mortierella indohii</i> C.Y. Chien 1974		G	Anastasi <i>et al.</i> (2002)
<i>Mortierella polycephala</i> Coemans 1863		G	Domsch (1960a)
<i>Mortierella reticulata</i> van Tieghem & le Monnier 1873	m	A	Breitenbach (1998)
<i>Mortierella</i> sp.	m	B, G, X	Von Klopotek (1962); Anastasi <i>et al.</i> (2002)
<i>Mortierella stylospora</i> Dixon-Stewart 1932	m	A	Breitenbach (1998)
<i>Mortierella turficola</i> Ling Young 1930	m	A	Breitenbach (1998)
<i>Mortierella vinacea</i> Dixon-Stewart 1932	m	A	Breitenbach (1998)
<i>Mucor abundans</i> Povah 1917	m	H	Eastwood (1952)
<i>Mucor caninus</i> Persoon 1796	m	O	Upreti and Joshi (1984)
<i>Mucor circinelloides</i> van Tieghem 1875	m	A	Breitenbach (1998)
<i>Mucor circinelloides</i> f. <i>circinelloides</i> van Tieghem 1875	m	B, G, P	Domsch (1960a); Von Klopotek (1962); Domsch <i>et al.</i> (1993)
<i>Mucor circinelloides</i> f. <i>griseocyanus</i> (Hagem) Schipper 1970		X	Anastasi <i>et al.</i> (2002)
<i>Mucor circinelloides</i> f. <i>janssenii</i> (Lendner) Schipper 1971 (syn.: <i>Circinella tenella</i> (Ling Young) Zycha 1935)	m	B	Von Klopotek (1962)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Mucor fragilis</i> Bainier sensu Zycha 1884	m	O	Upreti and Joshi (1984)
<i>Mucor hiemalis</i> Wehmer 1903	m	A	Breitenbach (1998)
<i>Mucor microsporus</i> Namyslowski 1910	m	A	Breitenbach (1998)
<i>Mucor miehei</i> Cooney & Emerson 1964	t	O	Upreti and Joshi (1984)
<i>Mucor plumbeus</i> Bonorden 1864 (syn.: <i>Mucor spinescens</i> Lendner 1907)	m	H	Eastwood (1952)
<i>Mucor pusillus</i> Lindt 1886	t	E, O	de Bertoldi <i>et al.</i> (1983); Upreti and Joshi (1984)
<i>Mucor racemosus</i> Fresenius 1850	m	A, O	Upreti and Joshi (1984); Breitenbach (1998)
<i>Mucor racemosus</i> f. <i>racemosus</i> Fresenius 1850 (syn.: <i>Mucor varians</i> Pišpek 1929)	m	H	Eastwood (1952)
<i>Mucor</i> sp.	m, t	A, B, M, O, U	Von Klopotek (1962); Fermor <i>et al.</i> (1979); Strauch (1987); Chung and Hoitink (1990); Ryckeboer <i>et al.</i> (2003)
<i>Myceliophthora</i> sp.		X	Anastasi <i>et al.</i> (2002)
<i>Myceliophthora thermophila</i> (Apinis) van Oorschot 1977 (syn.: <i>Sporotrichum thermophilum</i> Apinis)	t	J, X	Chang and Hudson (1967); Anastasi <i>et al.</i> (2002)
<i>Mycena</i> sp.	m	B	Von Klopotek (1962)
<i>Mycogone nigra</i> (Morgan) Jensen	m	B	Von Klopotek (1962); Golueke (1977)
<i>Myrothecium</i> sp.	m	O	Upreti and Joshi (1984)
<i>Nectria inventa</i> Pethybridge 1919		G	Domsch (1960a)
<i>Nectria</i> sp.		G	Anastasi <i>et al.</i> (2002)
<i>Nectria ventricosa</i> C. Booth 1971		G	Domsch (1960a)
<i>Neosartorya spinosa</i> (Raper & Fennell) Kozakiewicz 1989		X	Anastasi <i>et al.</i> (2002)
<i>Neosartorya fischeri</i> var. <i>fischeri</i> (Wehmer) Malloch & Cain		X	Anastasi <i>et al.</i> (2002)
<i>Nigrospora</i> sp.	m	N	Seck and Kilbertus (1996)
<i>Oedocephalum glomerulosum</i> (Bulliard: Fries) Saccardo	m	B, O	Von Klopotek (1962); Botha <i>et al.</i> (1990)

(continued)

TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Oedocephalum</i> sp.	m	A, B, O	Von Klopotek (1962); Fagan and Fergus (1984); Breitenbach (1998)
<i>Oidiodendron griseum</i> Robak 1934		G	Domsch (1960a)
<i>Oidium</i> sp.	t	P	Waksman <i>et al.</i> (1939a)
<i>Oospora variabilis</i> (Lindner) Lindau	m	H	Eastwood (1952)
<i>Paecilomyces farinosus</i> (Holm: Fries) A.H.S. Brown & G. Smith 1957		G	Anastasi <i>et al.</i> (2002)
<i>Paecilomyces fulvus</i> Stolk & Samson 1971	m	A	Breitenbach (1998)
<i>Paecilomyces inflatus</i> (Burnside) Carmichael 1962	m	A	Breitenbach (1998)
<i>Paecilomyces lilacinus</i> (Thom) Samson 1974		G	Domsch (1960a)
<i>Paecilomyces</i> sp.	m, t	A, E, O, P	Henssen (1957); de Bertoldi <i>et al.</i> (1983); Breitenbach (1998); Tuomela <i>et al.</i> (2000)
<i>Paecilomyces variotii</i> Bainier 1907	m, t	A, B, G, O, X	Von Klopotek (1962); Knoesel and Resz (1973); Upreti and Joshi (1984); Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Papulaspora immersa</i> Hotson 1912	m	A, P	Domsch <i>et al.</i> (1993); Breitenbach (1998)
<i>Panaeolus</i> sp.	m	B	Von Klopotek (1962)
<i>Penicillium albidum</i> Sopp 1912	m	A	Breitenbach (1998)
<i>Penicillium aurantiogriseum</i> Dierckx 1901 (syn.: <i>Penicillium martensii</i> Biourge 1923)	m	A	Breitenbach (1998)
<i>Penicillium aurantiogriseum</i> var. <i>aurantiogriseum</i> Dierckx (syn: <i>P. verrucosum</i> var. <i>cyclopium</i> (Westling) Samson <i>et al.</i> 1976)		G, X	Domsch (1960a); Anastasi <i>et al.</i> (2002)
<i>Penicillium brevicompactum</i> Dierckx 1901		G, X	Domsch (1960a); Anastasi <i>et al.</i> (2002)
<i>Penicillium canescens</i> Sopp 1912		G	Anastasi <i>et al.</i> (2002)
<i>Penicillium chermesinum</i> Biourge 1923	m	U, X	Mergaert and Swings (1996); Anastasi <i>et al.</i> (2002)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Penicillium chrysogenum</i> Thom 1910 (syn.: <i>Penicillium notatum</i> Westling 1911)	m	A, G, O, X	Upreti and Joshi (1984); Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Penicillium citrinum</i> Thom 1910		G, X	Anastasi <i>et al.</i> (2002)
<i>Penicillium commune</i> Thom 1910 (syn.: <i>P. palitans</i> Westling 1911)	m	A	Breitenbach (1998)
<i>Penicillium corylophilum</i> Dierckx 1901	m	A, G	Domsch (1960a); Breitenbach (1998)
<i>Penicillium corymbiferum</i> Westling 1911	m	A	Breitenbach (1998)
<i>Penicillium crustosum</i> Thom 1930	m	A	Breitenbach (1998)
<i>Penicillium cyclopium</i> Westling 1911	m	A	Breitenbach (1998)
<i>Penicillium dierckxii</i> Biourge		G	Anastasi <i>et al.</i> (2002)
<i>Penicillium digitatum</i> (Persoon: Fries) Saccardo 1882	m	B, G, X	Von Klopotek (1962); Anastasi <i>et al.</i> (2002)
<i>Penicillium diversum</i> Raper & Fennell 1948		G	Anastasi <i>et al.</i> (2002)
<i>Penicillium dupontii</i> Griffon & Maublanc emend. Emerson 1949	t	B, E	Von Klopotek (1962); de Bertoldi <i>et al.</i> (1983)
<i>Penicillium echinulatum</i> var. <i>echinulatum</i> Raper & Thom ex Fassatiová		G, X	Anastasi <i>et al.</i> (2002)
<i>Penicillium expansum</i> Link 1821	m	A, G	Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Penicillium glabrum</i> (Wehmer) Westling 1911 (syn.: <i>Penicillium frequentans</i> Westling 1912)		G, X	Domsch (1960a); Anastasi <i>et al.</i> (2002)
<i>Penicillium glandicola</i> (Oudem.) Seifert & Samson 1986 (syn.: <i>Penicillium granulatum</i> Bainier 1905)		X	Anastasi <i>et al.</i> (2002)
<i>Penicillium implicatum</i> Biourge 1923		G, X	Anastasi <i>et al.</i> (2002)
<i>Penicillium herquei</i> Bainier & Sartory 1912		G, X	Anastasi <i>et al.</i> (2002)
<i>Penicillium islandicum</i> Sopp. 1912	m	O, X	Upreti and Joshi (1984); Anastasi <i>et al.</i> (2002)
<i>Penicillium italicum</i> Wehmer 1894		X	Anastasi <i>et al.</i> (2002)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Penicillium janczewskii</i> Zaleski 1927 (syn.: <i>Penicillium nigricans</i> Bainier ex Thom 1930)	m	G, O, X	Domsch (1960a); Upreti and Joshi (1984); Anastasi <i>et al.</i> (2002)
<i>Penicillium jensenii</i> Zaleski 1927		G, X	Anastasi <i>et al.</i> (2002)
<i>Penicillium melinii</i> Thom 1930	m	A	Breitenbach (1998)
<i>Penicillium miczynskii</i> Zalewski 1927	m	A	Breitenbach (1998)
<i>Penicillium minioluteum</i> Dierckx 1901		G	Anastasi <i>et al.</i> (2002)
<i>Penicillium ochrochloron</i> Biourge 1923	m	A, G, U	Mergaert and Swings (1996); Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Penicillium oxalicum</i> Currie & Thom 1915	m	A, O	Fagan and Fergus (1984); Breitenbach (1998)
<i>Penicillium paxilli</i> Bainier 1907		G	Anastasi <i>et al.</i> (2002)
<i>Penicillium piceum</i> Raper & Fennell 1948		G, X	Anastasi <i>et al.</i> (2002)
<i>Penicillium purpurescens</i> (Sopp) Raper & Thom		X	Anastasi <i>et al.</i> (2002)
<i>Penicillium purpurogenum</i> Stoll 1904		G, X	Anastasi <i>et al.</i> (2002)
<i>Penicillium restrictum</i> Gilman & Abbott 1927		G, X	Anastasi <i>et al.</i> (2002)
<i>Penicillium rolsii</i> var. <i>rolsii</i> Thom		G	Anastasi <i>et al.</i> (2002)
<i>Penicillium roqueforti</i> Thom 1906	m	A, G	Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Penicillium roseopurpureum</i> Dierckx 1901		G, X	Anastasi <i>et al.</i> (2002)
<i>Penicillium rubrum</i> Stoll 1904		G	Domsch (1960a)
<i>Penicillium rugulosum</i> Thom 1910		X	Anastasi <i>et al.</i> (2002)
<i>Penicillium simplicissimum</i> (Oudemans) Thom 1930	m	G, U, X	Mergaert <i>et al.</i> (1994a); Mergaert and Swings (1996); Anastasi <i>et al.</i> (2002)
<i>Penicillium</i> sp.	m, t	A, B, E, G, H, J, M, N, O, S, U, X, Y	Eastwood (1952); Von Klopotek (1962); Chang and Hudson (1967); Fermor <i>et al.</i> (1979); de Bertoldi <i>et al.</i> (1983); Strauch and de Bertoldi (1985); Chung and Hoitink (1990); Hadar and Gorodecki (1991); Breitenbach (1998); Seck and Kilbertus (1996); Chamuris <i>et al.</i> (2000); Anastasi <i>et al.</i> (2002); Rocha <i>et al.</i> (2002); J. Ryckeboer, unpublished data

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Penicillium spinulosum</i> Thom 1910	m	A, X	Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Penicillium stoloniferum</i> Thom 1910	m	A	Breitenbach (1998)
<i>Penicillium velutinum</i> van Beyma 1935	m	A	Breitenbach (1998)
<i>Penicillium verrucosum</i> var. <i>verrucosum</i> Dierckx 1901		G	Anastasi <i>et al.</i> (2002)
<i>Penicillium viridicatum</i> Westling 1911	m	A	Breitenbach (1998)
<i>Penicillium waksmanii</i> Zaleski 1927	m	A, G, X	Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Peziza ostracoderma</i> Korf 1961		G	Domsch (1960a)
<i>Peziza vesiculosa</i> Bulliard: Fries 1789		O	Fagan and Fergus (1984)
<i>Phialemonium obovatum</i> W. Gams & McGinnis 1983		G	Anastasi <i>et al.</i> (2002)
<i>Phialophora cyclaminis</i> van Beyma 1942		X	Anastasi <i>et al.</i> (2002)
<i>Phoma exigua</i> var. <i>exigua</i> Desmazières 1849		X	Anastasi <i>et al.</i> (2002)
<i>Phoma glomerata</i> (Corda) Wollenweber & Hochapfel 1936 (syn.: <i>P. alternariacea</i> Brooks & Searle)	m	B	Von Klopotek (1962)
<i>Phoma herbarum</i> Westendorp 1852	m	G	Domsch (1960a)
<i>Phoma</i> sp.	m	B, X, Y	Von Klopotek (1962); Anastasi <i>et al.</i> (2002); Rocha <i>et al.</i> (2002)
<i>Phomopsis</i> sp.		G, X	Anastasi <i>et al.</i> (2002)
<i>Pichia</i> sp.	m	Y	Rocha <i>et al.</i> (2002)
<i>Piptocephalis</i> sp.	m	B	Von Klopotek (1962)
<i>Phthomyces</i> sp.	m	N	Seck and Kilbertus (1996)
<i>Plectosporium tabacinum</i> (van Beyma) M.E. Palm, W. Gams & Nirenberg 1995 (syn.: <i>Fusarium tabacinum</i> (van Beyma) W. Gams 1968)	m	A, X	Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Pleurotus ostreatus</i> (Jacquin: Fries) Kummer	m	E	de Bertoldi <i>et al.</i> (1983)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Preussia fleischhakkii</i> (Auerswald) Cain 1961		G, X	Domsch (1960b); Anastasi <i>et al.</i> (2002)
<i>Preussia</i> sp.		X	Anastasi <i>et al.</i> (2002)
<i>Pseudallescheria boydii</i> (Shear) McGinnis <i>et al.</i> 1982 (syn.: <i>Petriellidium boydii</i> (Shear) Malloch 1970)	m	B, G, X	Von Klopotek (1962); Anastasi <i>et al.</i> (2002)
<i>Pseudeurotium zonatum</i> van Beyma 1937		G	Domsch (1960a)
<i>Pseudogymnoascus roseus</i> Raillio 1929 (<i>P. vinaceus</i> Raillio 1929)	m	B	Von Klopotek (1962)
<i>Pullularia</i> sp.	m	B	Von Klopotek (1962)
<i>Pythium irregulare</i> Buisman 1927	m	A	Breitenbach (1998)
<i>Pythium oligandrum</i> Drechsler 1930	m	A	Breitenbach (1998)
<i>Rhinoctadiella atrovirens</i> Nannfeldt 1934	m	E	de Bertoldi <i>et al.</i> (1983)
<i>Rhizomucor pusillus</i> (Lindt) Schipper 1978 (syn.: <i>Mucor pusillus</i> Lindt 1886)	m, t	B, G, J, O, P	Von Klopotek (1962); Cooney and Emerson (1964); Fergus (1964); Chang and Hudson (1967); Fergus and Amelung (1971); Eicker (1972); Kane and Mullins (1973); Knoesel and Resz (1973); Fermor <i>et al.</i> (1979)
<i>Rhizomucor</i> sp.	t	M	Campbell <i>et al.</i> (1990)
<i>Rhizopus arrhizus</i> Fischer 1892	m	A	Breitenbach (1998)
<i>Rhizopus chinensis</i> Saito 1904	t	O	Upreti and Joshi (1984)
<i>Rhizopus microsporus</i> van Tieghem 1875	t	O	Upreti and Joshi (1984)
<i>Rhizopus oryzae</i> Went & Prinsen Geerligs 1895		G	Anastasi <i>et al.</i> (2002)
<i>Rhizopus stolonifer</i> (Ehrenb. ex Link) Lind 1913 (syn.: <i>Rhizopus nigricans</i> Ehrenberg 1820)	m	B, G, O	Domsch (1960a); Von Klopotek (1962); Upreti and Joshi (1984)
<i>Rhodotorula</i> sp.	m	N, Y	Strauch (1987); Seck and Kilbertus (1996); Rocha <i>et al.</i> (2002)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Rollandina capitata</i> Patouillard		G	Anastasi <i>et al.</i> (2002)
<i>Scedosporium apiospermum</i> Saccardo ex Castellani & Chalmers (syn.: <i>Monosporium apiospermum</i> Saccardo 1911)	m	B	Von Klopotek (1962)
<i>Scolecobasidium tshawytschae</i> (Doty & Slater) McGinnis & Ajello 1974 (syn.: <i>Ochroconis tshawytschae</i> (Doty & Slater) Krylenko & Al-Achmed 1977)	m	B	Domsch <i>et al.</i> (1993)
<i>Scopulariopsis brevicaulis</i> (Saccardo) Bainier 1907	m	A, B, E, G	Domsch (1960a); Von Klopotek (1962); de Bertoldi <i>et al.</i> (1983); Upreti and Joshi (1984); Breitenbach (1998); Anastasi <i>et al.</i> (2002); Ryckeboer <i>et al.</i> (2003); J. Ryckeboer, unpublished data
<i>Scopulariopsis brumptii</i> Salvanet-Duval 1935	m	G, X	Domsch (1960a); Anastasi <i>et al.</i> (2002)
<i>Scopulariopsis candida</i> (Guéguen) Vuillemin 1911	m	A, G, X	Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Scopulariopsis chartarum</i> (G. Smith) Morton & Smith 1963	m	A, G	Breitenbach (1998); J. Ryckeboer, unpublished data
<i>Scopulariopsis fusca</i> Zach 1934	m	G	Domsch (1960a)
<i>Scopulariopsis koningii</i> (Oudemans) Vuillemin 1911		G, X	Anastasi <i>et al.</i> (2002)
<i>Scopulariopsis</i> sp.	m	A, B, E	Von Klopotek (1962); de Bertoldi <i>et al.</i> (1983); Ryckeboer <i>et al.</i> (2003); J. Ryckeboer, unpublished data
<i>Scopulariopsis sphaerospora</i> Zach 1934		X	Anastasi <i>et al.</i> (2002)
<i>Scytalidium lignicola</i> Pesante 1957		G	Anastasi <i>et al.</i> (2002)
<i>Scytalidium thermophilum</i> ^a (Cooney & Emerson) Austwick 1976 (syn.: <i>Torula thermophila</i> ^a Cooney & Emerson)	t	B, E, O	Fergus (1969); Kane and Mullins (1973); de Bertoldi <i>et al.</i> (1983); Upreti and Joshi (1984); Wiegant (1992); Straatsma and Samson (1993); Straatsma <i>et al.</i> (1994)
<i>Sepedonium chrysospermum</i> (Bulliard: Fries) Link 1832	m	G	Chamuris <i>et al.</i> (2000)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Sepedonium niveum</i> Massee & Salmon	m	O	Botha <i>et al.</i> (1990)
<i>Sepedonium</i> sp.	m, t	B, P	Waksman <i>et al.</i> (1939a); Von Klopotek (1962)
<i>Sistotrema brinkmannii</i> (Bresadola) John Eriksson 1948 (syn.: <i>Corticium coronilla</i> von Höhnelt & Litschauer 1906)	m	B	Von Klopotek (1962)
<i>Sordaria fimicola</i> (Roberge) Cesati & de Notaris 1863	m	G	Domsch (1960a)
<i>Spicaria</i> sp.	m	B	Von Klopotek (1962)
<i>Sporotrichum</i> sp.	t	P	Henssen (1957)
<i>Sporotrichum thermophile</i> Apinis 1963	m, t	E, O	de Bertoldi <i>et al.</i> (1983); Upreti and Joshi (1984); Campbell <i>et al.</i> (1990)
<i>Sporothrix schenckii</i> Hektoen & Perkins 1900	m	A	Breitenbach (1998)
<i>Stachybotrys chartarum</i> (Ehrenberg) S.J. Hughes 1958 (syn.: <i>Stachybotrys alternans</i> Bonorden)	m	B, G, X	Domsch (1960a); Von Klopotek (1962); Anastasi <i>et al.</i> (2002)
<i>Stachybotrys</i> sp.	m	E, U	Golueke (1977); de Bertoldi <i>et al.</i> (1983)
<i>Staphylotrichum coccosporum</i> J.A. Meyer & Nicot 1956		G, X	Anastasi <i>et al.</i> (2002)
<i>Stemphylium</i> sp.	m	B	Von Klopotek (1962)
<i>Stereum hirsutum</i> (Willdenow: Fries) Fries 1938	m	G	Chamuris <i>et al.</i> (2000)
<i>Stereum</i> sp.	m	G	Chamuris <i>et al.</i> (2000)
<i>Stibella thermophila</i> ^b Fergus	t	O	Fergus (1964); Campbell <i>et al.</i> (1990)
<i>Stylopaga</i> sp.	m	B	Von Klopotek (1962)
<i>Syncephalis</i> sp.	m	A	Breitenbach (1998)
<i>Syncephalastrum racemosum</i> Cohn ex Schroeter 1886		X	Anastasi <i>et al.</i> (2002)
<i>Talaromyces emersonii</i> Stolk 1965 (misapplied name: <i>Talaromyces</i> <i>duponti</i> (Griffon & Maublanc) Apinis 1963)	t	E, J, O	Fergus (1964); Chang and Hudson (1967); Golueke (1977)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Talaromyces flavus</i> (Klöcker) Stolk & Samson 1972 (anamorph: <i>Penicillium dangeardii</i> Pitt 1980)	t	G	Domsch (1960a)
<i>Talaromyces flavus</i> var. <i>flavus</i> (Klöcker) Stolk & Samson 1972		X	Anastasi <i>et al.</i> (2002)
<i>Talaromyces helicus</i> var. <i>helicus</i> (Raper & Fennell) C.R. Benjamin 1955		U, X	Domsch <i>et al.</i> (1993); Anastasi <i>et al.</i> (2002)
<i>Talaromyces helicus</i> var. <i>major</i> Stolk & Samson 1972		X	Anastasi <i>et al.</i> (2002)
<i>Talaromyces thermophilus</i> Stolk 1965	t	E, O	Fergus (1969); de Bertoldi <i>et al.</i> (1983); Straatsma <i>et al.</i> (1994)
<i>Talaromyces wortmannii</i> (Klöcker) C.R. Benjamin 1955	m	G	Domsch (1960a)
<i>Thermoascus aurantiacus</i>		B, U	Von Klopotek (1962); Kane and Mullins (1973); Domsch <i>et al.</i> (1993)
<i>Thermomyces lanuginosus</i> (Griffon & Maublanc) Tsiklinsky 1899 (syn.: <i>Humicola lanuginosa</i> (Griffon & Maublanc) Bunce 1961)	m, t	B, E, G, J	Von Klopotek (1962); Cooney and Emerson (1964); Fergus (1964); Chang and Hudson (1967); Kane and Mullins (1973); Knoesel and Resz (1973); Jodice <i>et al.</i> (1974); Golueke (1977); Fermor <i>et al.</i> (1979); de Bertoldi <i>et al.</i> (1983); Upreti and Joshi (1984); Anastasi <i>et al.</i> (2002)
<i>Thermomyces</i> sp.	t	M, P	Waksman <i>et al.</i> (1939a); Henssen (1957); Campbell <i>et al.</i> (1990)
<i>Thielavia basicola</i> Zopf 1871		X	Anastasi <i>et al.</i> (2002)
<i>Thielavia heterothallica</i> von Klopotek	t	J, J, U	Hedger and Hudson (1970); von Klopotek (1974); Domsch <i>et al.</i> (1993)
<i>Thielavia terrestris</i> (Apinis) Malloch & Cain 1972 (syn.: <i>Allescheria terrestris</i> Apinis 1963)	t	E, O	de Bertoldi <i>et al.</i> (1985); Straatsma <i>et al.</i> (1994)
<i>Thielaviopsis basicola</i> (Berkeley & Broome) Ferraris 1912 (syn.: <i>Chalara elegans</i> Nag Raj & Kendrick 1975)		G	Domsch (1960a)

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TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Thielaviopsis</i> sp.	m	G	J. Ryckeboer, unpublished data
<i>Thysanophora penicillioides</i> (Roumeguère) Kendrick 1961		X	Anastasi <i>et al.</i> (2002)
<i>Torulopsis</i> sp.		Y	Rocha <i>et al.</i> (2002)
<i>Trametes versicolor</i> (Linnaeus: Fries) Pilát (syn.: <i>Polyporeus versicolor</i> (Linnaeus: Fries) Fries 1821)	m	E	de Bertoldi <i>et al.</i> (1985)
<i>Trichocladium asperum</i> Harz 1871	m	A, G	Breitenbach (1998); Domsch (1960a)
<i>Trichoderma atroviride</i> P. Karsten	m	A	Breitenbach (1998)
<i>Trichoderma hamatum</i> (Bonorden) Bainier 1906	m	G, M	Hoitink (1990); Anastasi <i>et al.</i> (2002)
<i>Trichoderma harzianum</i> Rifai 1969		G	Anastasi <i>et al.</i> (2002)
<i>Trichoderma pseudokoningii</i> Rifai 1969	m	A	Breitenbach (1998)
<i>Trichoderma</i> sp.	m	N	Seck and Kilbertus (1996)
<i>Trichoderma viride</i> Persoon: Fries 1829 (syn.: <i>Trichoderma lignorum</i> (Tode) Harz)	m	B, E, G, H, O	Eastwood (1952); Von Klopotek (1962); Cook <i>et al.</i> (1967); Fermor <i>et al.</i> (1979); de Bertoldi <i>et al.</i> (1985); Upreti and Joshi (1984); Anastasi <i>et al.</i> (2002)
<i>Trichoderma virens</i> (Miller <i>et al.</i>) von Arx 1987	m	A	Breitenbach (1998)
<i>Trichosporon sporotrichoides</i> (van Oorschot) van Oorschot & de Hoog 1981 (syn.: <i>Trichosporiella sporotrichoides</i> van Oorschot 1980)		X	Anastasi <i>et al.</i> (2002)
<i>Trichophaea abundans</i> (Karsten) Boudier 1907		O	Fagan and Fergus (1984)
<i>Trichothecium</i> sp.	m	A, P	Waksman <i>et al.</i> (1939a); Ryckeboer <i>et al.</i> (2003)
<i>Trichothecium roseum</i> (Persoon: Fries) Link ex Gray 1821	m, t	B, G, O	Domsch (1960a); Von Klopotek (1962); Fergus (1969); Botha <i>et al.</i> (1990); Chamuris <i>et al.</i> (2000)
<i>Trichurus spiralis</i> Hasselbring 1900	m	A, G, O	Domsch (1960a); Fagan and Fergus (1984); Breitenbach (1998)

(continued)

TABLE 4 – Overview of fungi reported in compost and self-heating organic materials at mesophilic and thermophilic temperatures (*follow the previous page*)

Organism*	Temperature phase**	Source material***	Reference
<i>Trichurus terrophilus</i> Swift & Povah 1929	m	B	Von Klopotek (1962)
<i>Ulocladium</i> sp.	m	N	Seck and Kilbertus (1996)
<i>Ulocladium alternariae</i> (Cooke) E.G. Simmons 1967		G	Anastasi <i>et al.</i> (2002)
<i>Ulocladium consortiale</i> (von Thümen) E. Simmons 1967 (syn.: <i>Stemphylium ilicis</i> Tengwall)	m	A, B	Von Klopotek (1962); Breitenbach (1998)
<i>Verticillium lecanii</i> (Zimmerman) A.W. Viégas 1939 (syn.: <i>Acrostalagmus albus-minus</i> A. & R. Sartory & Meyer)	m	A, G, H, X	Eastwood (1952); Breitenbach (1998); Anastasi <i>et al.</i> (2002)
<i>Verticillium leptobactrum</i> W. Gams 1971	m	A	Mergaert <i>et al.</i> (1994a)
<i>Verticillium nigrescens</i> Pethybridge 1919		X	Anastasi <i>et al.</i> (2002)
<i>Verticillium</i> sp.	m	A, B, G	Von Klopotek (1962); Chamuris <i>et al.</i> (2000); Ryckeboer <i>et al.</i> (2003)
<i>Volutella ciliata</i> (Albertini & Schweinitz: Fries 1832	m	G	Domsch (1960a)
<i>Westerdykella dispersa</i> (Clum) Cejp & Milko 1955		X	Anastasi <i>et al.</i> (2002)
<i>Zygorhynchus</i> sp.	m	P	Waksman <i>et al.</i> (1939a)
<i>Zygorhynchus heterogamus</i> (Vuillemin) Vuillemin 1903	m	B	Cook <i>et al.</i> (1967)
<i>Zygorhynchus moelleri</i> Vuillemin 1903	m	A, J	Eastwood (1952); Breitenbach (1998)

All species presented in this table, except *C. krusei* and *C. tropicalis*, were isolated on rich organic complex media.

* The most recent names are given. When older synonyms were cited in the referenced literature, these are given in parenthesis.

** Temperature phase: m = mesophilic; t = thermophilic; fungi are classified as mesophiles and thermophiles if their optimal growth temperatures are moderate (20-40 °C) or high (>40 °C), respectively.

*** Source material of compost: A = vegetable, fruit and garden waste; B = municipal solid waste; C = food waste and sawdust; D = kitchen waste and shredded newspapers; E = garden and kitchen waste and sewage sludge; F = grass (lawn cuttings); G = garden waste; H = lawn cuttings and barley straw; J = wheat straw, barley straw, straw compost; L = 70% green waste + 10% kitchen waste + 20% shredded wood; M = tree bark, hardwood bark, bark compost; N = peanut shells; O = mushroom compost; P = manure, horse manure; S = grape marc; U = unknown origin of compost; T = waste paper; X = vermicompost; Y = cattle manure and forestry wastes.

^a*Scytalidium thermophilum*, *Humicola grisea* var. *thermoidea*, *Humicola insolens* and *Torula thermophila* are synonyms (Straatsma and Samson, 1993).

^b*Stibella thermophila* is redescribed and transferred to a new anamorph genus, *Remersonia* (Seifert *et al.*, 1997).

them to degrade tough debris such as woody stems, bark or newspaper. Cellulose and hemicellulose originating from plant material, chitin from fungi and soil fauna and possibly lignin and humus are their C and N sources (Lacey, 1973; Hardy and Sivasithamparam, 1989; Beffa *et al.*, 1996b). There is also increasing evidence of their ability to degrade xenobiotic compounds (Goodfellow and Williams, 1983). Actinomycetes develop poorly in materials that are too wet (Finstein and Morris, 1975) or too dry (Festenstein *et al.*, 1965). Most actinomycetes tolerate a higher pH than fungi, their optimum pH is situated between 7 and 8 (Fermor *et al.*, 1979). Under adverse conditions actinomycetes survive as spores (Cross, 1968).

Thermal inactivation of pathogens is required to obtain safe products, both in terms of phytohygiene and human diseases. Thermal destruction of pathogens depends to a large degree on the species; lag-, exponential-, and asymptotic inactivation kinetics are known (Haug, 1993). Generally, the higher the temperature, the more efficient will be the destruction of pathogens (Ryckeboer *et al.*, 2002a). On the other hand Millner *et al.* (1987) reported that *Salmonella spp.* was suppressed more efficiently in composts produced at 55 °C than in those produced at 70 °C, indicating that in certain cases antagonistic effects exerted through other microorganisms, in many cases actinomycetes, may be more important than a high temperature. Additionally, regrowth of mesophilic populations may be delayed if too high temperatures are maintained for a long time and if this temperature is reached throughout the composting material (which is a goal to provide proper hygienisation). Appropriate reinoculation schemes have to be used to avoid this problem.

In the early thermophilic composting phase microorganisms start to metabolize proteins, increasing liberation of ammonium and causing subsequent alkalinization (de Bertoldi *et al.*, 1985; Thambirajah *et al.*, 1995). Compared with the initial mesophilic phase, degradation is accelerated (Fogarty and Tuovinen, 1991). Mesophilic microorganisms are inactivated or killed during the initial thermophilic phase (temperatures between 40-60 °C), whereas the numbers and species diversity of thermophilic and/or thermotolerant bacteria, actinomycetes and fungi increase (Waksman, 1939a; Finstein and Morris, 1975; Beffa *et al.*, 1996b). However, overall bacterial species diversity drops significantly during the thermophilic phase (Finstein and Morris, 1975; Fogarty and Tuovinen, 1991).

Typical bacteria that are very active at temperatures around 50-60 °C are endospore-forming bacteria, e.g. *Bacillus spp.* (Strom, 1985a, b; Beffa *et al.*, 1996c; Herrmann and Shann, 1997; Ryckeboer *et al.*, 2003). At temperatures above 60 °C, the degradation process is performed essentially by thermophilic bacteria (Gray *et al.*, 1971; Finstein and Morris, 1975; Bagstam, 1979; Nakasaki *et al.*, 1985a; Strom, 1985a,b; Fujio and Kume, 1991; Beffa *et al.*, 1996b). Non-spore forming bacteria such as *Hydrogenobacter spp.* and *Thermus spp.* are the dominant active degraders in thermogenic composts at temperatures above 70 °C, even upto 82 °C (Beffa *et al.*, 1996b, c; Blanc *et al.*, 1999). The number and diversity of thermophilic actinomycetes increases significantly at temperatures of 45 to 55 °C which are optimal for their growth (Waksman, 1939a; Fergus, 1964; Finstein and Morris, 1975; Nakasaki *et al.*, 1985a; Amner *et al.*, 1988; Beffa *et al.*, 1996b). In the preparation of mushroom (*Agaricus*) substrates, the so-called "firefang period" at 45-48 °C is known when the substrate is covered by a white actinomycete mycelium. The main function is a re-assimilation of ammonium, which does not occur in later stages. If the firefang period is too short or incomplete, ammonia will

later hamper the growth of *Agaricus*. To which extent similar processes occur in ordinary waste composting is not known. At temperatures above 60 °C, the number and diversity of actinomycetes decreases along with their importance in the degradation process.

Both thermophiles and mesophiles are reported to be good decomposers of cellulose, although the cellulose degrading ability of thermophiles was found to be exceedingly higher. The optimal temperature for cellulose degradation is around 65 °C, indicating that degradation is performed essentially by thermostable enzymes (Stutzenberger *et al.*, 1970; Upreti and Joshi, 1984). In Table 5, several prokaryotes are listed which are known to have cellulolytic activity (Fergus, 1969; Stutzenberger *et al.*, 1970; Godden *et al.*, 1989; Couglan and Mayer, 1992).

The ability of fungi to degrade cellulose and lignin is higher than that of actinomycetes, and bacteria in general (Crawford, 1983; Godden *et al.*, 1992). Temperature is one of the most important factors affecting fungal growth. The majority of fungi is mesophilic (5 °C to 37 °C), with an optimum temperature of 25-30 °C. Although most fungi prefer a moderate level of N, a low N content is a prerequisite for lignin degradation. Fungi mostly prefer an acidic environment (Fogarty and Tuovinen, 1991), although they often tolerate a wide range of pH (Tuomela *et al.*, 2000). Due to their extensive hyphal network, they can attack organic residues that are too dry, too acidic, or too low in nitrogen for bacterial decomposition (Finstein and Morris, 1975). Thermophilic fungi are generally less tolerant to high temperatures than actinomycetes. The optimal temperature for thermophilic fungi is 40 to 55 °C, with a maximum at 60 to 62 °C. At temperatures above 60 °C, fungi are killed or transiently present as spores (Eastwood, 1952; Von Klopotek, 1962; Kane and Mullins, 1973; Finstein and Morris, 1975; Rosenberg, 1975; Nakasaki *et al.*, 1985a; Fujio and Kume, 1991; Beffa *et al.*, 1996b; Ryckeboer *et al.*, 2003; Van Gestel *et al.*, 2003). Yeasts disappear during the thermophilic phase of composting, but when the temperature cools down to 54 °C, they can be found again (Choi and Park, 1998; Ryckeboer *et al.*, 2003). Table 6 lists several fungal genera which are able to degrade (crystalline) cellulose, carboxymethyl cellulose (CMC), hemicellulose, or more specific, xylan and arabinoxylan (Fergus, 1969; Fagan and Fergus, 1984; Botha *et al.*, 1990; Domsch *et al.*, 1993).

In mushroom compost, thermophilic fungi are responsible for the degradation of lignocellulose, which is prerequisite for the growth of the edible fungus (Sharma, 1989). The optimum temperature for thermophilic fungi from 40 to 50 °C is also the optimum temperature for lignin degradation in compost. The organisms most efficient at mineralizing lignin i.e. white-rot fungi, do not survive the thermophilic phase of composting, and thus cannot play a significant role in lignin degradation. A few Basidiomycota grow well at elevated temperatures, for example the white-rot fungus *Phanerochaete chrysosporium* (anamorph *Sporotrichum pulverulentum*) which has an optimum temperature around 36 to 40 °C and a maximum temperature of 46 to 49 °C (Tuomela *et al.*, 2000). At mesophilic temperatures degradation is partly continued by mesophilic fungi, although several authors report that negligible degradation occurred during compost maturation (Chang, 1967; Tomati *et al.*, 1995; Nusbaumer *et al.*, 1996). Examples of fungi reported to degrade chitin, pectin or keratin are listed in Table 6 (Domsch *et al.*, 1993).

The thermophilic phase *per se* is what composting differentiates from common degradation processes. Generally, higher temperatures accelerate biological

TABLE 5 – Known degradation capacity of genera of prokaryotes isolated from compost

Genus*	Degraded compound					
	Cellulose	Xylan	Lignin	Hydrocarbons	Pesticides	Bioplastics
	Reference list**	a	b	c	e	f
<i>Achromobacter</i>				+	+	
<i>Acidovorax</i>						+
<i>Acinetobacter</i>				+		
<i>Alcaligenes</i>			+	+		
<i>Amphibacillus</i>		+				
<i>Arthrobacter</i>	+		+	+	+	
<i>Bacillus</i>	+		+			+
<i>Brevibacillus</i>						+
<i>Brevibacterium</i>	+					
<i>Cellulomonas</i>	+					
<i>Clostridium</i>	+					
<i>Corynebacterium</i>			+	+		
<i>Cytophaga</i>	+					
<i>Enterobacter</i>			+			
<i>Flavobacterium</i>	+			+	+	+
<i>Klebsiella</i>			+			
<i>Micrococcus</i>				+		
<i>Micromonospora</i>	+		+			
<i>Nocardia</i>			+	+		
<i>Paenibacillus</i>	+					
<i>Pseudomonas</i>			+	+	+	+
<i>Pseudonocardia</i>	+		+			
<i>Rhodococcus</i>			+	+		
<i>Saccharomonospora</i>			+			
<i>Serratia</i>	+					
<i>Streptomyces</i>	+		+			+
<i>Thermoactinomyces</i>	+					
<i>Thermomonospora</i>	+		+			

* Different species within the several genera may show different reactions for one or more of the substrates. Within a species great differences may exist between different isolates.

** a: Fergus (1969); Stutzenberger *et al.* (1970); Godden *et al.* (1989); Coughlan and Mayer (1992).

b: Bachmann and McCarthy (1989); Nimura *et al.* (1990).

c: Deschamps *et al.* (1980); Goodfellow and Williams (1983); Gonzalez *et al.* (1986); Corominas *et al.* (1987); Falcon *et al.* (1987); McCarthy (1987); Tuomela *et al.* (2000).

d: Raymond and Jamison (1971); Jensen (1975); Rosenberg *et al.* (1980); Goodfellow and Williams (1983); Dragun (1988).

e: Fogarty and Tuovinen (1991).

f: Mergaert *et al.* (1994a,1994b); Mergaert and Swings (1996).

TABLE 6 – Known degradation capacity of fungal genera isolated from compost

Genus*	Degraded compound												
	Starch	Cellulose	CMC-Cellulose	Hemi-Cellulose	Xylan	Arabinoxylan	Lignin	Wood	Chitin	Pectin	Keratin	Hydrocarbons	Bioplastics
Reference list**	a	b	c	d	e	f	g	h	i	i	i	j	k
<i>Absidia</i>			+		+	+			+				
<i>Acremonium</i>		+	+		+							+	+
<i>Actinomucor</i>	+				+								
<i>Agaricus</i>	+	+	+	+	+		+						
<i>Alternaria</i>	+	+			+	+	+	+		+		+	
<i>Arthrinium, Scytalidium, Sordaria</i>		+											
<i>Arthrobotrys</i>		+	+		+								
<i>Aspergillus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Aureobasidium</i>								+					
<i>Beauvaria, Phanerochaete, Scolecobasidium</i>												+	
<i>Botryotrichum</i>	+	+	+		+		+	+	+				
<i>Botrytis</i>			+			+	+						
<i>Cephalosporium</i>													+
<i>Chaetomidium, Thermoascus</i>		+						+					
<i>Chaetomium</i>	+	+	+	+	+			+				+	
<i>Chrysosporium</i>		+									+		
<i>Cladosporium</i>	+	+				+	+			+		+	+
<i>Clitopilus, Sporotrichum</i>		+		+									
<i>Coniothyrium</i>					+			+		+			
<i>Coprinus</i>		+	+	+			+						
<i>Corynascus</i>		+	+		+	+							
<i>Doratomyces</i>	+	+	+	+	+		+	+					
<i>Emericella</i>	+	+	+			+						+	
<i>Epicoccum</i>		+			+	+	+	+		+			
<i>Fusarium</i>	+	+	+	+	+	+	+	+		+	+	+	
<i>Geotrichum</i>		+	+									+	
<i>Gilmaniella</i>	+	+	+		+			+					
<i>Gliocladium</i>	+	+	+		+			+	+	+		+	
<i>Humicola</i>		+	+	+				+					
<i>Malbranchea, Stibella</i>		+	+										
<i>Mortierella</i>									+			+	
<i>Mucor</i>	+		+	+	+		+		+	+		+	+
<i>Myceliophthora</i>											+		
<i>Nectria</i>	+	+					+	+	+	+			
<i>Oedocephalum</i>	+	+	+		+								
<i>Oidiodendron</i>	+	+						+					
<i>Paecilomyces</i>	+	+			+		+	+	+		+	+	
<i>Penicillium</i>	+	+	+		+		+			+		+	+
<i>Peziza, Volutella</i>	+	+	+										
<i>Phoma</i>	+	+	+		+			+		+		+	

(continued)

TABLE 6 – Known degradation capacity of fungal genera isolated from compost (*follow the previous page*)

Genus*	Degraded compound												
	Starch	Cellulose	CMC-Cellulose	Hemi-Cellulose	Xylan	Arabinoxylan	Lignin	Wood	Chitin	Pectin	Keratin	Hydrocarbons	Bioplastics
Reference list**	a	b	c	d	e	f	g	h	i	i	i	j	k
<i>Preussia</i>							+						
<i>Pseudeurotium, Pseudogymnoascus</i>					+								
<i>Rhizomucor</i>	+	+				+				+			
<i>Rhizopus</i>	+	+		+					+	+			
<i>Scopulariopsis</i>	+	+			+	+	+		+			+	+
<i>Sepedonium</i>	+	+	+	+	+								
<i>Sporotrichum</i>		+	+	+						+			
<i>Stachybotrys</i>		+						+	+	+			
<i>Talaromyces</i>	+	+	+	+			+	+				+	
<i>Thermomyces</i>		+		+		+							
<i>Thielavia</i>		+					+	+					
<i>Trichocladium</i>	+	+								+			
<i>Trichoderma</i>	+	+	+		+	+	+	+	+		+	+	
<i>Trichophaea</i>		+	+		+								
<i>Trichothecium</i>	+	+	+	+	+	+			+	+			
<i>Trichurus</i>	+	+	+		+			+				+	
<i>Ulocladium</i>		+				+		+					
<i>Verticillium</i>	+	+							+	+		+	+
<i>Zygorhynchys</i>				+						+			

* Different species within the several genera may show different reactions for one or more of the substrates. Within a species great differences may exist between different isolates.

** a: Fagan and Fergus (1984); Diaz-Ravina *et al.* (1989); Botha *et al.* (1990); Domsch *et al.* (1993); Atkinson *et al.* (1996b).

b: Chang (1967); Fergus (1969); Stutzenberger *et al.* (1976); Upreti and Joshi (1984); Fagan and Fergus (1984); Botha *et al.* (1990); Domsch *et al.* (1993); Tuomela *et al.* (2000); Rocha *et al.* (2002).

c: Fergus (1969); Fagan and Fergus (1984); Botha *et al.* (1990); Domsch *et al.* (1993); Tuomela *et al.* (2000).

d: Chang (1967); Fagan and Fergus (1984); Lynch and Wood (1985); Botha *et al.* (1990); Domsch *et al.* (1993); Tuomela *et al.* (2000).

e: Fagan and Fergus (1984); Botha *et al.* (1990); Domsch *et al.* (1993).

f: Domsch *et al.* (1993).

g: Fagan and Fergus (1984); Lynch and Wood (1985); Domsch *et al.* (1993); Tuomela *et al.* (2000); Chamuris *et al.* (2000).

h: Fagan and Fergus (1984); Domsch *et al.* (1993); Tuomela *et al.* (2000).

i: Domsch *et al.* (1993); Anastasi *et al.* (2002).

j: Llanos and Kjoller (1976); Davies and Westlake (1979); Dragun (1988); Aust (1990); McFarland *et al.* (1992); Domsch *et al.* (1993); Van Gestel *et al.* (2003).

k: Mergaert *et al.* (1994a); Mergaert and Swings (1996).

processes and improve hygienisation; thus, it may be assumed that the maximum temperatures should be as high as possible. However, there are some limitations. Oxygen can be supplied to the interior of composting piles by molecular diffusion and (more importantly) by mass movement through air pores (either through convection or forced aeration). Gas saturation constants decrease with increasing temperature so that O₂ availability for the microbial cells is limited at high temperatures. Some authors state that at temperatures above 60°C functional biodiversity is reduced and thus degradation processes may be hampered (Jeris and Regan, 1973; Suler and Finstein, 1977; McKinely and Vestal, 1984; de Bertoldi *et al.*, 1985; McKinely *et al.*, 1985). For *Geobacillus stearothermophilus*, one of the most typical thermophiles in composts it is known that the cell size increases at high temperatures, while at the same time the thickness of the aqueous biofilms decreases. Thus, at some point, *G. stearothermophilus* activity may be impaired.

In the opinion of several researchers, exceeding optimal temperature during composting will not shorten the composting period neither will it eliminate nuisances nor improve product quality beyond the genetic capacity of the microorganisms (de Bertoldi *et al.*, 1985; Golueke, 1992).

Cooling or second mesophilic phase

Once the activity of the thermophilic organisms ceases due to exhaustion of substrates, the temperature starts to decrease. Mesophilic organisms start to re-colonise the substrate, either originating from surviving spores, through spread from protected microniches, or from external inoculation. Upon initial temperature decrease the bacterial numbers may decrease by 1 to 2 orders of magnitude in comparison with the numbers present during the thermophilic phase (10^8 - 10^{11} g⁻¹ dry wt), but the taxonomic and metabolic diversity increase. Several bacterial functions that are important for compost maturation and which are absent or not detected in the thermophilic phase appear during the cooling and maturation phase (Beffa *et al.*, 1996b). Metabolic studies revealed that several isolates were not simply organic oxidizers, but were involved in hydrogen-, ammonium-, nitrite- and sulfur-oxidation, nitrogen-fixation, sulfate-reduction, exopolysaccharide production, and nitrite production from ammonium under heterotrophic conditions (Diaz-Ravina *et al.*, 1989; Beffa *et al.*, 1996b). High numbers of diverse mesophilic and thermotolerant actinomycetes and yeasts reappear (Herrmann and Shann, 1997). The temperature decline, the lower water content and their ability to attack and/or degrade natural complex polymers (e.g. cellulose, hemicellulose, lignocellulose, lignin) also favor mesophilic and thermotolerant fungi during the cooling phase (Waksman *et al.*, 1939a; Savage *et al.*, 1973; Finstein and Morris, 1975; Breitenbach, 1998; Chamuris *et al.*, 2000; Ryckeboer *et al.*, 2003).

Maturation phase

Tree bark, yard wastes, agricultural wastes, etc. contain a high percentage of lignin, lignocellulose and other recalcitrant components (Corominas *et al.*, 1987; Hoitink and Boehm, 1999). Paper may contain up to 20% of lignin (Tuomela *et al.*, 2000). Mainly during the maturation phase, these more resistant compounds are degraded and partly transformed into humus (Gray *et al.*, 1971; Crawford, 1983; Corominas *et al.*, 1987; Falcon *et al.*, 1987; Hoitink and Boehm, 1999; Tuomela *et al.*, 2000). Most of the fungi, predominant cellulose and lignin degraders, are isolated during

the maturation phase (Von Klopotek, 1962). One problem arising with composting as a means of solid waste disposal is the presence of undegraded cellulosic material in the compost at the end of the process. This residual cellulose is probably inaccessible to enzymatic attack because of low water content or association with protective substances such as lignin (ligno-cellulose complexes) (Stutzenberger *et al.*, 1970; Poincelot and Day, 1973).

Knowledge of the microbial composition and the microbial populations, involved in the nutrient cycles (i.e. C, N, S, P) in mature composts, is important to predict its potential impact on soil fertility and other biological parameters. Bacteria related to the genus *Arthrobacter* form a numerically important fraction of the natural bacterial flora of soils and their presence and numbers in mature composts could be used as an additional microbiological parameter for compost maturity evaluation. Species diversity seems to be correlated with stability of the end product (Beffa *et al.*, 1996b). Furthermore, the degree of maturity of the compost affects its successful utilization in agriculture. Immature composts induce high microbial activity in the soil some time after their incorporation, causing oxygen deficiency and a variety of indirect phytotoxicity problems to plant roots (Zucconi *et al.*, 1981a, 1981b; Inbar *et al.*, 1990). Maturity tests are discussed in detail by Itävaara *et al.* (2002) and Insam and de Bertoldi (2003). Benefits of compost application, such as suppression of diseases caused by soilborne plant pathogens, in agricultural and horticultural crops have been reported previously (Lacey, 1973; Hoitink and Fahy, 1986; Dick and McCoy, 1993; Hoitink and Boehm, 1999; Ryckeboer *et al.*, 1999; Ryckeboer, 2001).

AN INVENTORY OF COMPOST MICROORGANISMS

The majority of the microorganisms described in Tables 3 and 4 were isolated by culturing of extracts on agar media. Approximately half of the listed species in both tables grows at high temperatures. Most of the reported actinomycetes are thermophilic or thermotolerant, while most of the reported fungi are mesophilic. Knowledge on specific functions of taxonomic groups and species is still fragmentary. In cases where evidence for certain degradation capacities during a composting process is clear, this is indicated in Tables 5 and 6.

The inventory contains 155 species of prokaryotes (of which 33 strains were reported as actinomycetes) belonging to 66 genera, and 408 fungal species of 160 genera. The majority of isolates (approximately 80 species of prokaryotes and 295 fungal species) had been isolated from (source-separated) municipal, kitchen, grass, yard and agricultural wastes or their respective composts. Thirty-three species of prokaryotes and 82 fungal species were found in mushroom compost, while 121 fungal species were isolated from vermicompost. Eighteen species of prokaryotes and 18 fungal species have been found in manure. Sixteen species of prokaryotes and 12 fungal species were isolated from bark or bark compost, while 26 species of fungi have been found in straw or straw compost. A few more species of prokaryotes were found in sewage sludge and moldy hay, while a few fungal species are reported in grape marc, peanut shells and other food wastes. Some of the substrates also included considerable amounts of shredded newspaper or leaves. All these materials were major or minor input components of the composting process.

It needs to be emphasized that within the genera, different species may show different reactions for one or more of the substrates and also that within a species great differences may exist between different isolates.

CONCLUSIONS AND OUTLOOK

Several of the organisms may find applications as potential biocontrol agents of soilborne plant pathogens, among them bacteria (Table 3), e.g. *Flavobacterium balustinum*, *Bacillus subtilis*, *Bacillus cereus* and *Pseudomonas fluorescens* (Hoitink and Fahy, 1986; Hoitink, 1990; Phae and Shoda, 1990; Phae *et al.*, 1990; Wei *et al.*, 1991; Asaka and Shoda, 1996; Nakasaki *et al.*, 1996; Raupach and Kloepper, 1998; Ryckeboer *et al.*, 1999; Ryckeboer *et al.*, 2002b) and fungi (Table 4) such as *Trichoderma* spp., *Gliocladium virens* and *Paecilomyces* spp. (Domsch, 1960a; Hoitink and Boehm, 1999; Ryckeboer *et al.*, 1999; Ryckeboer *et al.*, 2002b). Potential human pathogens e.g. *Alcaligenes faecalis*, *Clostridium* spp. and *Aspergillus fumigatus* (Eastwood, 1952; Von Klopotek, 1962; Fergus, 1964; Chang and Hudson, 1967; Stutzenberger *et al.*, 1970; Kane and Mullins, 1973; Knoesel and Resz, 1973; Malik and Sandhu, 1973; Fermor *et al.*, 1979; Strom, 1985b; Campbell *et al.*, 1990; Beffa *et al.*, 1996a; Lott Fischer *et al.*, 1996) are also listed in Tables 3 and 4.

From the literature and the brief survey of the degradation capacities of prokaryotes and fungi listed above we can conclude that the ability to degrade monosaccharides, starch and lipids is almost universal among fungi and prokaryotes (Botha *et al.*, 1990). Hemicelluloses and cellulose are also relatively fast degraded. More complex natural polymers (e.g. lignin and keratin), wood (lignocellulose), synthetic polymers (e.g. bioplastics) and hydrocarbons are mostly degraded by specialists of a limited number of genera. However, these abilities are mostly determined with single species tests, which often underestimate degradation capacities. Several reports on mixed populations clearly illustrated the synergistic effects of various organisms (Waksman and Hulpoi, 1939; Golueke, 1992; Tuomela *et al.*, 2000). Furthermore, the use of indicator substrates is also questionable. For example, the use of a substrate such as carboxymethyl cellulose (CMC) as an indicator of cellulolytic activity may be far removed from the natural situation where the substrate is much more complex, e.g. lignocellulosic material in which lignin and cellulose must be depolymerised simultaneously (Deschamps *et al.*, 1981; Davis *et al.*, 1992).

Most publications were targeted on a few species and on their specific activities. Indeed, there are only a few microbiological studies in which a full process was followed in detail (Von Klopotek, 1962; Strom, 1985a, 1985b; Beffa *et al.*, 1996b; Ryckeboer *et al.*, 2003; Van Gestel *et al.*, 2003).

Most of the former research was performed using culturing techniques (Kane and Mullins, 1973; Finstein and Morris, 1975; Nakasaki *et al.*, 1985a; Strom 1985a, 1985b; Hardy and Sivasithamparam, 1989; Davis *et al.*, 1991; Beffa *et al.*, 1996a; Choi and Park, 1998). It is estimated for soils that less than 1% of the viable microbiota is cultivable with current techniques (Torsvik *et al.*, 1990). For composts the percentage is unknown, and molecular techniques suggest that also in composts numerous microorganisms prevail that currently cannot be isolated (Ivors

et al., 2000). Peters *et al.* (2000) characterised several prokaryotes in a composting pile containing shredded maize plants, straw-bedded horse manure and wood chips, by direct analysis of DNA, i.e. without culturing on agar media. In this composting pile *Azotobacter salinestris*, *Bacillus badius*, *Bacillus coagulans*, *Bacillus fusiformis*, *Bacillus smithii*, *Clostridium stercoarium* subsp. *thermolacticum* (syn.: *Clostridium thermolacticum*), *Geobacillus caldoolyolyticus* (syn.: *Bacillus caldoolyolyticus*), *Geobacillus stearothermophilus* (syn.: *Bacillus stearothermophilus*), *Geobacillus thermocatenulatus* (syn.: *B. thermocatenulatus*), *Geobacillus thermoleovorans* (syn.: *B. thermoleovorans*), *Lactobacillus confuses*, *Lactobacillus panis*, *Pseudomonas citronellolis*, *Pseudomonas stutzeri*, *Streptomyces thermodiasticus*, *Streptosporangium vulgare*, *Thermobispora bispora* (syn.: *Microbispora bispora*), *Thiobacillus denitrificans* (*B. denitrificans*) and *Xanthomonas campestris* were identified. However, of this list, only *B. badius*, *B. coagulans*, *B. smithii*, *G. stearothermophilus* and *P. stutzeri* were reported yet in composting materials after isolation on agar media (Table 3) (Strom, 1985b; Fermor *et al.*, 1979; Hoitink and Fahy, 1986; Fujio and Kume, 1991; Andrews and Trevors, 1994; Koschinsky *et al.*, 1998; Ryckeboer *et al.*, 2003; J. Mergaert, unpublished data).

From a few references we can conclude that the combination of cultivation-dependent and -independent approaches will yield complementary, non-overlapping information about the composition of the microbial community in compost (Gurtner *et al.*, 2000; Ivors *et al.*, 2000; Dees and Ghiorse, 2001, Mannix *et al.*, 2001; van Elsas *et al.*, 2002).

Contradictory reports exist concerning the usefulness of targeted inoculation of the starting material of composts to accelerate the composting process itself (Finstein and Morris, 1975). However, several studies have shown that it is possible under certain circumstances (Bagstam, 1979; Choi and Park, 1998). A better understanding of how the microbial communities change during composting and which environmental conditions they require could facilitate controlled composting. Such manipulations could be used to alleviate composting odours (Finstein and Morris, 1975), to increase available nutrients (Beffa *et al.*, 1996b; Ivors *et al.*, 2000), to increase efficacy of biofiltration techniques for removing toxic organic compounds from gaseous waste streams, e.g. benzene, toluene, xylenes and trichloroethylene (Watwood and Sukesan, 1995; Tahraoui and Rho, 1998; Juteau *et al.*, 1999), or even, speculatively, open the possibility to produce desired secondary metabolites. Composting could also be used to increase degradation of pesticides (Fogarty and Tuovinen, 1991; Lemmon and Pylypiw, 1992; Michel *et al.*, 1995, 1997a; Brown *et al.*, 1997; Buyuksonmez *et al.*, 2000), complex natural polymers, e.g. lignin (Lynch, 1987; Requena *et al.*, 1996, 1997; Chamuris *et al.*, 2000; Tuomela *et al.*, 2000), bioplastics (Mergaert *et al.*, 1994a, 1994b; Mergaert and Swings, 1996; Kleeberg *et al.*, 1998; Rick *et al.*, 1998) and (polyaromatic) hydrocarbons (McFarland *et al.*, 1992; Berger and Schwartz, 1994; Civilini, 1994; Riggle, 1995; Kästner *et al.*, 1995; Silveira and Ganho, 1995; Civilini and Sebastianutto, 1996; Hupe *et al.*, 1996; Sukesan and Watwood, 1998; Löser *et al.*, 1999; Van Gestel *et al.*, 2003). Among the various biological niches found during a composting process, there are likely some that facilitate the degradation of xenobiotic compounds. Care, however, has to be taken that temperature dependent volatilization of compounds is not mistaken as biodegradation (Van Gestel *et al.*, 2003).

Polymers designed to undergo biological degradation are often proposed to solve problems arising from plastic waste. Standardized test methods using mixed cultures for the evaluation of biodegradability and compostability have been suggested, including *in-situ* composting tests as well as *in vitro* tests with pure cultures (Kleeberg *et al.*, 1998). Examples of microorganisms reported to degrade bioplastics such as poly(3-hydroxybutyrate) are also listed in Tables 5 and 6 (Delafield *et al.*, 1965; Mergaert *et al.*, 1994a,1994b; Mergaert and Swings, 1996).

A relatively new research field is the use of composts as an organic carrier for antagonists, i.e. microorganisms with biocontrol properties (Nakasaka *et al.*, 1996; Ryckeboer *et al.*, 2002b). Such manipulations could be used to better suppress plant diseases (Kwok *et al.*, 1987; Phae *et al.*, 1990; Hoitink *et al.*, 1991; Grebus *et al.*, 1994; Hoitink and Boehm, 1999; Ryckeboer *et al.*, 1999). The establishment of inoculated organisms requires abiotic factors to be at least within the tolerance range, and the appropriate niche to be either unfilled or filled with less efficient organisms (Finstain and Morris, 1975; Hoitink and Fahy, 1986).

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