Major Habitats and Diversity of Thermophilic Fungi

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Swapnil Chaturvedi and Indira P. Sarethy

Abstract

More than 80% of the earth surface has extreme environmental conditions, not conducive for normal life, as assessed on anthropogenic parameters. Along with the discovery of novel bacteria and archaea from various extreme environments, it has been found that fungi also are capable of colonizing such areas. These fungi have been shown to have diverse phylogenetic characteristics, belonging to many genera. Conditions of extremes of pH, temperature, pressure, and radiation necessitate special strategies for survival, involving genetic changes, which can result in novel natural products. Thermophilic fungi occurrence is generally in soil or in habitats where decomposition of plant material such as grains, compost, husk, municipal refuse, and other organic material takes place, under humid and aerobic environment conditions. In these habitats, thermophiles occur as either resting propagules or as active mycelia depending on the nutrients and environmental condition. The occurrence of thermophilic fungi is due to the dissemination of propagules from masses of organic material. Thermophilic fungi belong to various genera such as *Zygomycetes*, *Ascomycetes*, and *Deuteromycetes*. Metabolites from these organisms, not found in normal habitats, can be of good value. Based on the biological activity and structure of compounds isolated from such extremophilic fungi, more than 150 compounds have been documented from thermophilic species of *Penicillium*, *Aspergillus*, and others. The current chapter focuses on the major habitats of thermophilic fungi, their ecology, physiology, and molecular biology, elicitation of specialized metabolites from them, and their various documented activities.

S. Chaturvedi · I. P. Sarethy (✉)
Department of Biotechnology, Jaypee Institute of Information Technology, Noida, Uttar Pradesh, India
e-mail: indirap.sarethy@jiit.ac.in

S. Sahay (ed.), *Extremophilic Fungi*, https://doi.org/10.1007/978-981-16-4907-3_3

Keywords

Thermophilic fungi · Extremophilic fungi · Metabolites · Metagenomics

3.1 Introduction

Thermophilic fungi are eukaryotic organisms, which generally grow at temperatures of 60–62 °C. According to Cooney and Emerson (1964), thermophiles are divided into three categories: thermophiles grow at above 45 °C, extreme thermophiles 66–79 °C, and hyperthermophiles 80 °C (Maria et al. 2016). Thermophilic fungi grow at above 45 °C and above, and the minimum temperature for growth is 20 °C (Oliveria et al. 2015). They occur in soil or in habitats where decomposing plant materials such as grains, compost, husk, municipal refuse, and other organic material are present. In these habitats, thermophiles occur as either resting propagules or as active mycelia depend on the nutrients and the environmental conditions. These fungi are spread by the dissemination of propagules from masses of organic material. They belong to genera such as *Zygomycetes*, *Ascomycetes*, and *Deuteromycetes.* They have a role in the production of thermostable enzymes and are used as components of recombinant organisms for the production of proteases, pectinases, and cellulases (Surrough et al. 2012). Thermophilic fungi can be cultivated in the laboratory on different media such as yeast-starch agar (YpSs), oatmeal agar (OA), and Czapek's agar (C3) as expounded by Cooney and Emerson (1964). *Themomyces stellatus* can grow at above 45 °C (Morgenstern et al. 2012). These fungi contain saturated fatty acids (Maheshwari et al. 2000) and can survive in stress conditions such as high water pressure and desiccation (Mahajan et al. 1986). Thermophilic fungi have an important role to play in environment as they can degrade organic matter, act as biodeteriorants by producing intracellular and extracellular enzymes, phenolic compounds, polysaccharides, antibiotics, and can also serve as single-cell protein (SCP). Single-cell proteins can act as bioconversion agents, for instance such as in preparation of mushroom compost. *Chaetomium* and *Pulverulentum* produce SCP from lignocellulosic wastes. *Chaetomium thermophile* and *Humicola lanuginose* compost are rich in different minerals such as sodium, potassium, and phosphorus. Thermophilic activities of microbes are associated with the thermostability of enzymes and proteins. Advantages of using these thermostable enzymes and protein are reduction in contamination risk of mesophilic microbes in industrial processes and products; as the viscosity of culture medium decreases, solubility of organic compounds increases and as the coefficient of diffusion of reactant and product increases, the rate of reaction becomes higher.

3.2 Types

Thermophilic fungi grow at temperatures between 25 and 80 °C, which is associated with biological conditions. According to Cooney and Emerson (1964), the maximum temperature for their growth is above 50 °C and minimum 25 °C.

Based on various studies, some terms are given to thermophilic fungi to further categorize them:

1. Thermophilic: Fungi that grow at or above 45 °C (Maheshwari et al. 2000).
2. Thermotolerant: Those that grow best at a maximum of 50 °C and minimum of 20 °C (Mouchacca 2000).
3. Thermophilius fungi: They include both thermophilic and thermotolerant fungi (Apinis 1963).
4. Thermoduric fungi: Fungi whose reproductive structures can resist temperature of 80 °C or above, but normal growth is at 22–25 °C (Apinis and Pugh 1967).
5. Transitional thermophile*:* Fungi that grow below 20 °C but can survive at temperature up to 40 °C (Apinis and Pugh 1967).
6. Stenothermal: Those that grow at a narrow temperature range mostly found in a habitat with a constant temperature range (Brock and Fred 1982).
7. Eurythermal: Fungi that grow at a wider temperature range mostly found in the habitat where temperature fluctuates (Brock and Fred 1982).

3.3 History

Earlier studies on thermophilic fungi were more focused on their occurrence in various habitats. The first thermophilic hyphomycetes, *Thermomyces lanuginosus*, was reported from potato and described by Tsiklinskaya (1899). Four thermophilic fungi, *Thermoidium sulphureum*, *Mucor pusillus*, *Thermoascus aurantiacus*, and *Thermomyces lanuginosus*, are based on the growth of thermophilic fungi to the thermogenesis of agriculture stock by Miehe (1907). Later he also studied the thermophilic and mesophilic fungi to check the maximum temperature for their growth. Led Kurt Noack (1920) isolated thermophilic fungi from different natural substrates and observed that thermophilic fungi are present in habitats with varying temperatures. Allen and Emerson (1949) isolated many thermophilic fungi, which were able to grow at 60 °C. They found that thermophilic microflora in retting guayule decreased the amount of resin in the extract of crude rubber, which resulted in improved physical properties. In 1950, La Touche discovered new cellulolytic ascomycetes, which had industrial applications. Notable publications on thermophilic fungi during the sixties and seventies included ones by Apinis (1963), Eggins and Malik (1969) for temperate climate soil, and Hedger (1974) and Gochenaur (1975) for tropical regions. Morphology of thermophilic fungi is based on their biological activities, which help in the discovery of industrial application. Approximately 75 types of thermophilic fungi species have been discovered till now, comprising around 0.1% of the total fungal species, from compost, soil, desert soil, wood husk, organic material and coal, and many more.

3.4 Habitats

Several extreme conditions are found in the environment such as large or small temperature ranges, acidity, radiation, and drought conditions; few organisms are able to survive in these conditions, with a vast majority unable to adapt to such variations. Thermophilic fungi prefer composts, snuff, municipal waste, wood husk, grains, and other such organic material where the preferred humidity and aerobic environmental conditions are present for their growth and development. Figure 3.1 shows various habitats from where thermophilic fungi have been isolated. Table 3.1 shows that the earliest studies of thermophilic fungi, which have shown these to be

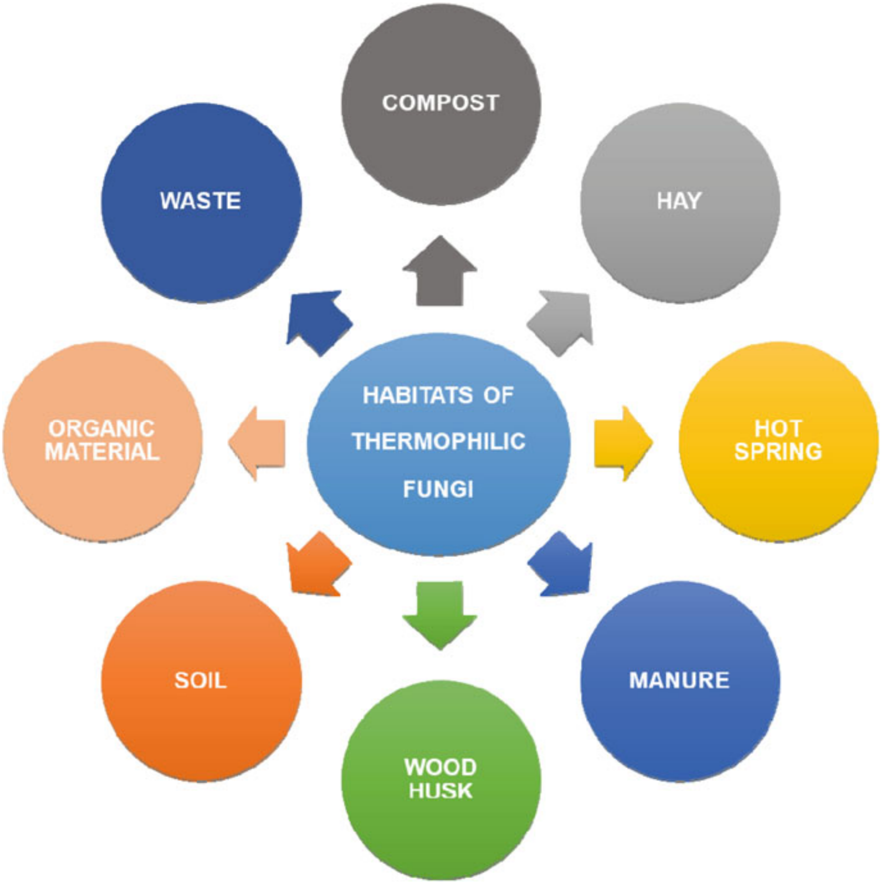

Fig. 3.1 Habitats from where thermophilic fungi have been isolated

Table 3.1 Origin of thermophilic fungi and their habitats

Class	Organism	Habitat	Reference
Ascomycetes	*Canariomyces thermophile*	Soil	von Arx et al. (1988)
	Chaetomium britannicum	Mushroom compost, soil	Ames (1963), Chen and Chen (1996)
	Chaetomidium pingtungium	Sugarcane field Decomposing leaves	Ames (1963)
	Chaetomium virginicum	Plant remains, seeds of *Capsicum annuum*, soil	Ames (1963)
	Chaetomium senegalensis	Soil, decomposing wheat straw	Ames (1963)
	Corynascus sepedonium	Soil, pasture soil, hay, coal spoil tips, compost	von Arx (1975)
	Coonemeria crustacean	Coal spoil tips, bagasse, soil	von Arx (1975)
	Thielavia australiensis	Nesting material of malleefowl	Tansey and Jack (1975)
	Talaromyces byssochlamydoides	Forest soil	Guarro et al. (1996)
Zygomycetes	*Rhizomucor pusillus*	Municipal wastes, horse dung, composted wheat straw, guayule, hay, seeds of cacao, barley, maize and wheat, groundnuts	Schipper (1978)
	Rhizomucor miehei	Soil, sand, coal mines, hay, stored barley, compost	Cooney and Emerson (1964)
Eurotiomycetes	*Paecilomyces themophila*	Wheat straw	Yang et al. (2006)
	Malbranchea cinnamomea	Compost, soil	Maijala et al. (2012)
	Sporotrichum thermophile	Soil	Sadaf and Khare (2014)
Deuteromycetes	*Scytalidium thermophilum*	Compost, soil	Narain et al. (1983)
	Scytalidium thermophilum	Compost	Robledo et al. (2015)
	Acremonium thermophilum	Sugarcane bagasse	Van Oorschot (1977)
	Chrysosporium tropicum	Dung, soil, air	Gams and Lacey (1972), Carmichael (1962)
	Acremonium alabamense	Alluvial soil	Malloch and Cain (1973)

widely present in decomposing organic matter or hot springs, are still the habitats from where these continue to be isolated. In these habitats, thermophilic fungi may occur as resting or active mycelia depending upon the favorable conditions of the environment.

In 1939, Waksman and his team isolated thermophilic fungi from soil. As seen from Table 3.1, thermophilic fungi have been isolated from a wide variety of materials. Thermophilic fungi grow easily in temperate countries but not in tropical countries. Their occurrence is due to self-heating masses of organic material (Maheshwari et al. 1987). A thermophilic fungus was found in Australia in temperate soil region (Ellis and Keane 1981). Thirty-two thermophilic and thermotolerant fungi were found in coal soil with well-organized colonies (Evans 1971). Pine hardwood pine scrub (Ward Jr and Cowley 1972) were found to be good sources too. Approximately 75 types of thermophilic fungi species have been discovered till now, comprising around 0.1% of the total fungal species, from compost, soil, desert soil, wood husk, and organic material land coal.

3.4.1 Natural Habitats

In these habitats, where high temperature conditions prevail round the year, thermophilic fungi have been obtained using culture-dependent techniques. Some of the characteristics of these habitats and the fungi isolated are discussed in this section.

3.4.1.1 Hot Springs

This is a type of thermal spring generated from geothermally heated water. Water flows from hot spring and is heated either by geothermal process or when water flows from the hot rock surface. On the other hand, in volcanic areas, water gets heated on coming in contact with magma. Boiling water, which builds up steam pressure, which comes out in the form of jet on the earth surface, is called a geyser. Countries from which fungi have been documented from such hot springs are Canada, New Zealand, Japan, Chile, Hungary, Israel, India, and Fiji. Hot spring water contains many minerals, which provide the growth of microbiota. These hot spring thermal areas are niches with some unique qualities, which can be explored for biotechnological purposes. Isolation and characterization of thermophilic fungi from hot spring thermal regions have been done by several researchers in the past decades (Sharma et al. 2012). Thermophilic fungi are present in a larger population in the hot spring region of Indonesia, but all of them are not able to grow under the hot spring volcanic conditions and is restricted to some species. Five types of thermophilic fungi were isolated from WU-Rai of northern Taiwan: *Humicola insolens*, *Rhizoctonia*, *Aspergillus fumigatus*, *Penicillium dupontii*, and *Thermomyces lanuginosus*, all of which could grow between 55 and 65 °C (Chen et al. 2000). A research of the mycoflora in Yangmingshan National Park, northern Taiwan, from August 1999 to June 2000, of thermophilic and thermotolerant fungi inhabiting sulfurous hot spring soils, identified 12 taxa (Chen et al. 2003). Further four thermophilic fungi species were reported from Xiaoyoukeng sulfurous area:

Sporotrichum sp., *Chrysosporium* sp., *Scytalidium thermophilum*, and *Papulaspora thermophile*. Pan et al. (2010) isolated thermophilic fungi from geothermal sites with alkalescent hot spring in Tengchong Rehai National Park, China and utilized the ITS region Internal transcribed spacer) sequencing system to classify fungi. More than a hundred fungal strains were isolated such as *Talaromyces byssochlamydoides*, *Rhizomucor miehei*, *Thermoascus aurantiacus*, *Talaromyces thermophiles*, *Thermomyces lanuginosus*, *Scytalidium thermophilum*, and *Coprinopsis species*.

3.4.1.2 Soil

Soil is the upper land surface on earth, which is the mixture of all the organic material present with minerals and other components, which provide support for the growth of the organism. In soil, various microorganisms provide nutritious condition to plant and animal species. Thermophilic fungi grow in soil; however, it depends on the nature of the soil. According to researchers, such fungi are present in the upper layer of the soil or the debris of the plant on the soil; Rajasekaran and Maheshwari (1993) estimated the respiratory rates of thermophilic and mesophilic fungi. They discovered that the respiratory rate of thermophilic organisms was especially receptive to changes in temperature; however, that of mesophilic fungi was generally free of such changes, suggesting that in thermally fluctuating conditions thermophilic fungi might be at a physiological setback in contrast to mesophilic organisms. Their work shows that thermophilic fungi are inactive components of soil microflora. Different types of species were isolated from south-central Indiana soil, a sun-heated soil: *Myriococcum albomyces*, *Aspergillus fumigatus*, *Talaromyces thermophilus*, *Humicola lanuginosa*, *Allescheria terrestris*, *Malbranchea pulchella var. sulfurea*, *Thielavia heterothallica*, *Mucor pusillus*, *Chaetomium thermophile var. dissitum*, *Thielavia minor*, *Thermoascus aurantiacus*, *Mucor miehei*, *Torula thermophila*, *Humicola stellata*, *Acrophialophora nainana*, *Thielavia sepedonium*, *Dactylomyces thermophilus*, *Talaromyces emersonii* (Tansey and Jack 1976), *Malbranchea cinnamomea* (Maijala et al. 2012), and *Sporotrichum thermophile,* (Lu et al. 2013).

Ten species of thermophilic fungi was identified from different zones of Darjeeling in eastern Himalayan soil. It was observed that there was a decline in the pervasiveness of thermophiles with expanding altitudes (Sandhu and Singh 1981). Later, thermophilic and thermotolerant fungi were isolated from 77 regions of Iraq. Out of these, six were true species of thermophilic fungi, while the rest were thermotolerant. *Aspergillus terreus*, *A. fumigatus*, *and A. niger* were available with frequencies of the event of 70%, 68%, and 60%, individually, and thus the investigation revealed that thermophilic and thermotolerant fungi are widely present mycoflora of Iraq soils (Abdullah and Al-Bader 1990).

3.4.1.3 Desert Soil

Desert soil has the amount of precipitation that falls based on temperature or due to geographical location. Around one-third land surface of the earth is arid and semi-arid. Researchers have isolated thermophilic fungi from the desert where the temperature is up to 55 °C or above. However, water is required for the growth, even when spores are present in dry soil. Abdel-Hafez (1982) studied the desert soil of Saudi Arabia for thermophilic fungi and isolated 48 species of thermophilic fungi from 24 genera on different laboratory media such as Czapek's agar media and containing cellulose or glucose. The organisms isolated were *A. fumigatus*, *Humicola grisea var*, *Aspergillus nidulans*, and *C. thermophile var. copropile.* Further, it was reported that 16 species were reported: *Mucor pusillus*, *Talaromyces*, *Thielavia*, *Myxococcus*, *Stilbella thermophile*, *A. fumigatus*, *C. thermophile var. copropile*, *C. thermophile var. dissitum*, *Chaetomium virginicum*, *Torula thermophile*, *Malbranchia pulchella var. sulfurea*, *Malbranchia pulchella var. sulfurea*, *Sporotrichum pulverulentum*, *Talaromyces thermophilus*, *Myriococcum albomyces*, *Allescheria terrestris*, *Papulaspora thermophile*, *Sporotrichum pulverulentum*, and *Humicola lanuginose.* In Middle East region (Egypt, Iraq, Syria, and Kuwait) thermophilic and thermotolerant fungi from desert soil were isolated from which *Malbranchea cinnamomea*, *Scytalidium thermophilum*, *Myceliophthora thermophile*, and *Thermomyces lanuginosus* were obtained by Mouchacca (1995). Thermophilic fungi from the Thar desert of India were isolated such as *Aspergillus flavus*, *A. niger*, *A. terreus*, *A.versicolor*, *Chaetomium*, *Emericella*, *Emericellanidulans*, *Fusarium*, *Chlamydosporum*, *Penicillium*, *Scytalidium*, *Thanatephorus cucumeris*, *Cunninghamella*, *Eurotium*, *Mucor*, *Chrysogenum*, *Talaromyces*, *Alternaria alternata*, and *Rhizopus stolonifer* (Sharma et al. 2010). Eight thermophilic fungi were identified from desert area of Yard province: *Ulocladium*, *Fusarium*, *Penicillium*, *Aspergillus*, *Alternaria*, *Rhizopus*, *Stemphylium*, and *Paecilomyces* (Rafiei and Banihashemi 2019).

3.4.1.4 Coal Mine Soil

Thermophilic fungi were isolated from coal mine soil of Chandameta, Parasia, from Chhindwara District of Madhya Pradesh, India. The normal temperature and precipitation rate of this region is 21 °C and 64 cm. A total of 14 fungi species were isolated: *Achaetomium macrosporum*, *Emericella nidulans*, *Rhizopus rhizopodiformis*, *Absidia corymbifera*, *Thermomyces lanuginosus*, *Thielavia minor*, *Humicola grisea*, *Aspergillus fumigatus*, *Thermoascus aurantiacus*, *Torula thermophile*, *Rhizopus microsporus*, *Penicillium sp.*, *Sporotrichum sp.*, *and Aspergillus fumigatus* (Johri and Thakre 1975). Coal mine near Hazaribagh Jharkhand exhibited the presence of thermophilic and thermotolerant fungi such as *Chrysosporium tropicum*, *Melanocarpus albomyces*, *Chaetomium piluliferum*, *Chaetomium thermophile*, *Penicillium chrysogenum*, *Aspergillus fumigatus*, *Curvularia lunata*, and *Cladosporium* spp. (Tulsiyan et al. 2017).

3.4.1.5 Coal Soil Tips

Coal soil tip is waste accumulated together in one place. Thermophilic fungi can grow on coal soil tip easily isolated thermophilic fungi from coal soil tip and observed that thermophilic fungi grow in these habitats due to its high temperature, organic material waste, and lack of soil crumbs. More than 30 thermophilic fungi species from different genera were isolated: *Aspergillus, Penicillium, Rhizopus, Mucor, Chrysosporium, Acrophialophora, Aspergillus, Calcarisporium,* *Chrysosporium, Geotrichum, Penicillium, Scolecobasidium,* and *Talaromyces* (Evans 1971).

3.4.2 Man-Made Habitats

Man-made habitats are largely those created and lived in by human beings. These types of habitats having effluents, thermal insulation system, stored grains, and compost piles provide a suitable environment for growth of thermophilic fungi. Heating in these environments can be by natural means (such as the heat generated during decomposition) or provided artificially by solar heating or other self-heating systems in which temperature can rise to 70 °C.

3.4.2.1 Manure

It is an organic material that is obtained from human, animal, and plant residues. They contain nutrients in organic material form (Larney and Hao 2007). Agricultural processes require a high demand for manure, but as manure has directly come in contact with agricultural land, it may cause many adverse effects on soil, water, and nutrient leaching. Manure compost provides better nourishment to the product as they are rich in nutritious value. Holman et al. (2016) have isolated thermophilic fungi such as *Thermomyces lanuginosus* and *Remersonia thermophile.*

3.4.2.2 Municipal Waste

Municipal waste is the waste material that has lignocellulosic material and some inorganic waste material. According to a study by Kaiser et al. (1968), municipal corporations generate more than 50% paper waste. Stutzenberger and their group (1970) studied the microorganisms that could degrade lignocellulosic materials. In municipal waste, the temperature can rise to 60 °C, suitable for growth of thermophilic fungi. Kane and Mullins (1973) isolated *Torula thermophile*, *Humicola lanuginosa*, *Mucor pusillus*, *Aspergillus fumigatus*, *Chaetomium thermophilum*, and *Thermoascus aurantiacus*. Sen et al. (1979) studied thermophilic fungi such as *Mucor* and *Humicole*, which were rich in nutrients such as nitrogen, potassium, and phosphorus. From different parts of India, various representatives such as *Myceliophthora thermophile* and *Thermo mucor sp.* have been isolated. Thermotolerant fungi such as *Cladosporium* and *Absidial* spp. were isolated from municipal waste in Iran (Ghazifard et al. 2001).

3.4.2.3 Wood Chip Piles

Wood chip piles are strong pieces of wood made by cutting or chipping parts of freshly harvested wood and are commonly utilized for the production of wood mash and as a crude material for specialized wood handling. Brown et al. (1994) found that these wood chip pile consists more than 50% weight of water due to which bacteria can grow easily by a fermentation process. Tansey (1971) studied that as the temperature rises in these stored wood chip piles, an ignition process starts due to which growth of thermophilic fungi takes place, and this causes deterioration in wood quality. He also isolated thermophilic fungi from wood chip piles obtained from paper factory: *Humicola lanuginose, Chaetomium thermophile var. dissitum, Talaromyces emersonii, Chaetomium thermophile var. coprophile*, *Talaromyces thermophiles*, and *Sporotrichum thermophile.*

3.4.2.4 Hay

Hay is related to grass, vegetables, or different herbaceous plants that have been cut, dried, and put away as bundles for later use as grain, especially for nibbling creatures. The hay bundles are stacked one over another, and the moisture present in these lead to the growth of microorganisms. Miehe (1907) isolated *Thermoascus aurantiacus*, *Rhizomucor pusillus*, and *Thermomyces lanuginosus* from a self-heating haystack. After inoculating hay and other organic material with a pure culture of fungi, he observed that sterilized hay does not produce heat, whereas the inoculated fungus does generate heat. Gregory and Lacey (1963) found that a different type of microflora develops in haystack, which has some moisture content. They demonstrated that hay having a 16% moisture content heated up moderately, while that having 25% moisture heated up to 45 °C, allowing the development of thermotolerant molds. But the temperature in wet bales with 45% moisture soared to 60–65 °C, and a range of thermophilic fungi, including *Aspergillus fumigatus, Mucor pusillus, and Humicola lanuginose*, and some actinomycetes were also recovered. Thermophilic fungal strains are capable of growing at 50–60 °C, at pH 2.0. More than 70 fungal strains belonging to *Ascomyota* were isolated from decaying plant matter and compost (Thanh et al. 2019).

3.4.2.5 Stored Grains

Stored grains have been used for centuries to fulfill the requirement for food necessity. Tansey and Brock (1978) studied that thermophilic fungi, though present on grains, do not damage grains prior to storage. Stored grains are a good substrate for the colonization of thermophilic fungi. Clark (1967), Clarke (1969), and Lacey (1971) discovered various thermophilic fungi from stored grains such as *Aspergillus candidus*, *Absidia corymbifera*, *Humicola lanuginosa*, and *Mucor pusillus*. Mulinge and Apinis (1969) isolated *Eurotium amstelodami*, *Absidia spp*., *Monascus spp*., *Aspergillus fumigatus*, *Aspergillus terreus*, and *Dactylomyces crustaceus* from stored moist barley grains. Hansen and Welty (1970) isolated thermophilic fungi from cocoa beans. Wareing (1997) isolated the thermophilic and thermotolerant *Aspergillus flavus*, *Paecilomyces variotii*, *Rhizomucor pusillus*, *Thermomyces lanuginosus*, and *Thermoascus crustaceous* from stored maize grain in sub-Saharan Africa. *Thermomyces*, *Fumigatus*, *Dupontii*, *Thermomyces lanuginosces*, *Rhizomucor*, *and Thermoascus crustaceus* were obtained from corn grain at 52 °C (Sandona et al. 2019).

3.5 Biodiversity of Thermophilic Fungi

3.5.1 Zygomycetes

1. *Rhizomucor miehei* form colonies with sporangia at 40–45 °C. Initially colonies are white and later turn into gray–brown (Schipper 1978). Spherical sporangia are 30–60 μm in diameter. The zygospore is subspherical and initially reddish-brown, later turning a black color with a diameter of 30–50 μm. They are found on soil, coal mines, hay, stored barley, and compost. They have been studied and geographically found in the United States, India, Ghana, the United Kingdom, and Saudi Arabia (Salar and Aneja 2007).
2. *Rhizomucor nainitalensis* produces colonies with sporangiospores and grows at 48 °C and is very similar to *R. miehei*. Sporangiospores are ellipsoidal, dumb bell-shaped and 3–6 μm in diameter (Joshi 1982). They grow predominantly on decomposed oak log and mainly have been reported in tropical places such as India (Salar and Aneja 2007).
3. *Rhizopus rhizopodiformis* produces colonies and grows well at 45 °C. Initially colonies are white and later turn black (Thakre and Johri 1976). They have a hyphae structure 3–7 μm in diameter; sporangia are spherical with a smooth, black surface and 76–175 μm in diameter and are found in coal mine soils, nesting material of birds, bread, wooden slats, soil, seeds of *Lycopersicon esculentum*, and oil palm effluents. They are found in India, the United Kingdom, South Africa, China, Hong Kong, Indonesia, Malaysia, and Japan (Salar and Aneja 2007).

3.5.2 Ascomycetes

1. *Canariomyces thermophila* colonies grow at 45 °C under laboratory conditions (Von arx et al. 1988). Ascospores are dark colored and irregularly shaped with spore size 14.0–18.0 × 7.5–10.0 μm in diameter. They have been largely found in Africa (Salar and Aneja 2007).
2. *Chaetomidium pingtungium* have colonies that grow at 45–50 °C. They produce dark globose cleistothecia with thick hairy walls and are 2–5 μm wide and 350 μm long. Asci are cylindrical in shape with a diameter of 40–52 × 7–9 μm and have an 8-spored structure (Chen and Chen 1996). Ascospores are uniseriate, dark brown, and are thick-walled structures 8.5–10.0 × 6.5–8.5 μm diameter. They have been reported from sugarcane fields of Taiwan (Salar and Aneja 2007).
3. *Chaetomium britannicum* produces colonies that grow at 45–50 °C under laboratory conditions (Ames 1963). Ascomata are cylindrical in shape with a hairy surface. Ascospores are brown in color and irregularly shaped (19–24 × 11–14 μm diameter). They have been reported from mushroom compost and soil of the United Kingdom (Salar and Aneja 2007).
4. *Chaetomium mesopotamicum* has colonies that grow at 30–50 °C. They are different from other species (Abdullah and Zora 1993). It produces long and

highly branched structures and has been isolated from date palm in Iraq (Salar and Aneja 2007).

5. *Coonemeria aegyptiaca* produces colonies growing at 25–55 °C under laboratory conditions. Ascocarps are a crusty mass with red brown color during the initial growth phase and have a coiled hyphae structure. Ascospores are single celled and appear yellowish to pale reddish orange, are thick-walled and smooth. Conidiophores are produced on aerial hyphae, with a smooth-walled surface, and diameter of 50–300 × 5–7 μm with apical parts irregularly branched. Phialides are solitary or irregularly verticillate and cylindric structure, with diameter size 12–30 × 3–6 μm. They are usually found in soil and have been reported from Egypt and Iraq (Ueda and Udagawa) Mouchacca 1997; Salar and Aneja 2007).
6. *Melanocarpus thermophilus* has eight-spored asci (Guarro et al. 1996), with ascospores being ovoid, dark brown, 7.5–9.0 × 6.0–7.5 μm, and each provided with a single germ pore. This isolate has been reported from forest soil of Iraq (Salar and Aneja 2007).

3.5.3 Deuteromycetes

1. *Arthrinium pterospermum* colonies have been shown to grow at 37 °C. They have hyphae like structure 2 μm in diameter (Apinis 1963). Conidiogenous cells are colorless during the initial phase of growth and later become dark brown with a diameter size of 7.6 × 5.3 μm. These have been described from hay and soil in the USA (Salar and Aneja 2007).
2. *Myceliophthora thermophile* produces colonies at 45 °C. Colonies have floccose surface or granular (Van Oorschot 1977). Initially, they have white colored colonies, which subsequently turn brown with a diameter of 2 μm. These have been reported to grow in soil from various countries with diverse climatic conditions such as Canada, India, Japan, and Australia (Salar and Aneja 2007),
3. *Papulospora thermophila* colonies have two types of mycelia: those with an arrow diameter (1.5 μm) and those with a wider diameter (5–7 μm) and with highly branched structures (Fergus 1971). Bulbils are present on hyphae in the form of globes to subglobose with diameter of 105 × 90 μm. These hyphae have an irregular shape, and initially, they are yellow later orange in color. These have been reported from mushroom compost and soil in India and Japan (Salar and Aneja 2007).
4. *Scytalidium indonesicum* colonies grow at 45 ° C on laboratory media. Conidia are brown with barrel-shaped to ellipsoid shape; they have a thick wall surface with a diameter size 25–12 μm (Hedger et al. 1982). Once conidia are fully grown they form irregular shaped brown structures with thick wall. These have been reported from Indonesia (Salar and Aneja 2007).

3.6 Metagenomic Analyses of Thermophilic Fungi

Metagenomics-based analysis has considerable potential in understanding industrial applications of thermophiles. The general strategy of metagenomics utilizes both functional- and sequence-based techniques for a comprehensive understanding (Rodriguez et al. 2018). Thermophiles surviving above 55 °C have high potential for biotechnological applications for production of biocatalysts, which can be beneficial in reducing contaminations, especially in food industry. Thermoenzymes are efficient under high pH, temperature, pressure, and high concentration of substrate and hence are used in production of paper, textile, food, and pharmaceuticals (DeCastro et al. 2016). Table 3.2 shows some cellulases obtained from thermophilic fungi.

3.7 Metagenome-Based Classification

The classification of fungi in metagenomics studies is based on the Internal Transcribed Spacer (ITS) sequence obtained from next-generation sequencing data (Oliveria et al. 2015; Thanh et al. 2019). The so-obtained sequence data must be deposited in a public repository such as the National Centre for Biotechnology Information (NCBI). Table 3.3 shows the study of thermophilic fungi based on taxonomy and diversity. Different repositories and tools (http://www.indexfungorum.org/, http://www.mycobank.org/) are available where the description of each taxon is available based on their nomenclature and classification database. Many of the sequences obtained from such studies have been identified/tallied with appropriate MycoBank numbers, some of them mapped with fungi which had been identified considerably earlier. An example is *A. fumigatus*, identified in a study by Latge (1999), which has been mapped with an isolate identified in 1863.

3.8 Phylogenetic Analysis: Case Study

A case study of *Thermomyces lanuginosus* (Fig. 3.2) shows that many isolates of this species have been obtained, sequenced, and submitted in GenBank. A phylogenetic analysis using Mega X (Kumar et al. 2018) shows that the isolates map close to each other though many clades and subclades have formed. This indicates that considerable differences also exist among the isolates. This directly indicates possible genetic diversity among produced compounds such as enzymes and other metabolites too.

Table 3.2 Some cellulases obtained from thermophilic fungi

Enzyme	Optimum temperature (°C)	Optimum pH	Source	Reference
AtCel7A	60	5.0	*Acremonium thermophilum*	Voutilainen et al. (2008)
CBHI	55	3.0	*Aspergillus aculeatus*	Takada et al. (1998)
CtCel7A	65	4.0	*Chaetomium thermophilum*	Voutilainen et al. (2008)
CBH3	65	5.0	*Chaetomium thermophilum*	Li et al. (2006)
CBH1	55	5.0	*Humicola grisea* var. *thermoidea*	Takashima et al. (1998)
TeCel7A	55	4.0	*Talaromyces emersonii*	Voutilainen et al. (2010)
Cel7A	65	3.0	*Penicillium funiculosum*	Texier et al. (2012)
TaCel7A	55	5.0	*Thermoascus aurantiacus*	Voutilainen et al. (2008)
CBHI	65	6.0	*Trichoderma viride*	Song et al. (2010)
ThCBHI	50	5.0	*Trichoderma harzianum*	Colussi et al. (2011)
Bgl	60	5.0	*Fusarium oxysporum*	Zhao et al. (2013)
Bgl4	55	6.0	*Humicola grisea* var. *thermoidea* IFO9854	Takashima et al. (1999)
Bgl1	55	5.5	*Orpinomyces* sp. PC-2	Li et al. (2004)
Bgl1G5	50	6.0	*Phialophora* sp. G5	Li et al. (2013)
Cel3A	50–60	5.0	*Amnesia atro brunnea*	Colabardini et al. (2016)
Cel3B	50–60	5.0	*Amnesia atro brunnea*	Colabardini et al. (2016)
BglB	52	5.5	*Aspergillus nidulans*	Calza et al. (1985)
Bgl	50	5.0	*Aspergillus oryzae*	Tang et al. (2014).
MoCel3A	50	5.5	*Magnaporthe oryzae*	Takahashi et al. (2011)
MoCel3B	50	5.5	*Magnaporthe oryzae*	Takahashi et al. (2011)
NfBGL1	80	5.0	*Neosartorya fischeri*	Yang et al. (2014)
PtBglu3	75	6.0	*Paecilomyces thermophile*	Yan et al. (2012)
RmBglu3B	50	5.0	*Rhizomucor miehei*	Guo et al. (2015)
β-Glucosidase	75	4.5	*Talaromyces aculeatus*	Lee et al. (2013)
CBH1	55	5.5	*Fusarium lini*	Mishra et al. (1983)
CBH11	55	5.5	*Fusarium lini*	Mishra et al. (1983)

(continued)

Table 3.2 (continued)

Enzyme	Optimum temperature (°C)	Optimum pH	Source	Reference
S1	50	4.0	*Irpex lactus*	Kanda et al. (1980)
En1	50	5.0	*Irpex lactus*	Kanda et al. (1980)
E2A	60	5.0	*Irpex lactus*	Kubo and Nisizawa (1983)
E2B	60	5.0	*Irpex lactus*	Kubo and Nisizawa (1983)
GB1(E)	60	5.5	*Pyricularia oryzae*	Hirayama et al. (1978)
GB2(E)	45	5.0	*Pyricularia oryzae*	Hiramaya and Nagamaya (1979)

Table 3.3 Taxonomy of thermophilic fungi

Taxon name	MycoBank number	Reference
Aspergillus fumigatus	MB#211776	Latge (1999)
Chaetomium thermophilum	MB#807382	Amlacher et al. (2011)
Myceliophthora fergusii	MB#317954	van den Brink et al. (2012)
Myceliophthora heterothallica	MB#519877	Houbraken et al. (2011)
Myceliophthora guttulata	MB#802335	Zhang et al. (2014)
Rhizomucor miehei (=Mucor miehei)	MB#322483	Schipper (1978)
Rasamsonia byssochlamydoides	MB#519877	Houbraken et al. (2011)
Thermomyces dupontii	MB#805186	Houbraken et al. (2014)
Thermothelomyces heterothallica(=Myceliophthora heterothallica)	MB#809491	Stchigel et al. (2015)
Thermothelomyces thermophila (=Myceliophthora thermophila)	MB#809493	Stchigel et al. (2015)
Thermomyces lanuginosus (=Humicola lanuginosa)	MB#239786	Singh (2003)

3.9 Metabolites

Thermophilic and thermotolerant fungi are considered as good sources of thermostable enzymes, which can be useful in industrial processes that function at higher temperatures. A variety of thermostable enzymes have been obtained from thermophilic fungi such as cellulases, lipases amylases, and proteases (Thanh et al. 2019).

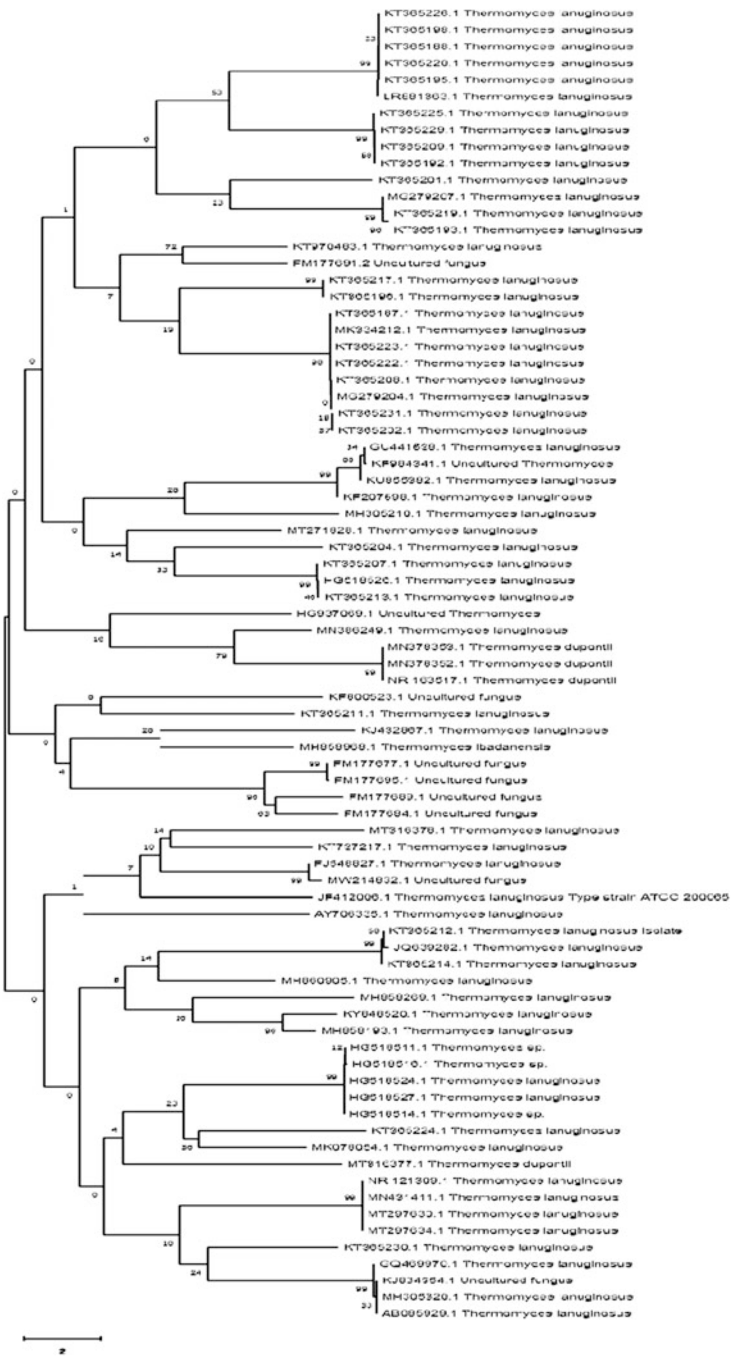

Fig. 3.2 Phylogenetic tree of 95 GenBank nucleotide sequences from isolates of *T. lanuginosus*. Branch lengths are in the same units as those of the evolutionary distances, computed using the Maximum Composite Likelihood method

Hence, the information provided in Sect. 3.8 can be relevant in further purifying and better understanding of more potentially novel thermo-stable enzymes, considering that many of the isolates of *T. lanuginosus* fall into distinct clades.

Many carbohydrate-active enzymes (CAZymes) have been found in thermophilic fungi. For example, four polysaccharide lyases (PLs), 28 carbohydrate esterases (CEs), and more than 50 enzymes with auxiliary activities (AAs) have been described. The genome of *Thielavia terrestris* has been shown to encode nearly 500 CAZymes, including 212 glycoside hydrolases (GHs), 91 glycosyl transferases (GTs), and 80 carbohydrate-binding modules (CBMs). Studies have shown that common strategies for thermal adaptation include a reduced genome size and increased frequency of the amino acids such as Ile, Val, Tyr, Trp, Arg, Glu, and Leu (IVYWREL) in proteins (Thanh et al. 2019), contributing to thermostability. *T. lanuginosus* has encouraging potential in production of xylanase too, as seen from its genetic sequence (Oliveria et al. 2015).

Orfali and Perveen (2019) isolated two new compounds - 3-(furan 12-carboxylic acid)-6-(methoxycarbonyl)-4-hydroxy-4-methyl-4 and 5-dihydro-2H-pyran 1 3-α-methyl-7-hydroxy-5-carboxylic acid methyl ester-1-indanone - from a thermophilic *Penicillium* species that was initially isolated from Ghamiqa hot spring sediments (Saudi Arabia). Austinol, emodin, and 2-methyl-penicinoline, already documented, were also isolated. Emodin showed cytotoxicity against HTB-176 cell line, while austinol exhibited antibacterial activity against *Pseudomonas aeruginosa.* It is interesting that new bioactive molecules are elicited from thermophilic fungi and need further studies.

Metabolite profiling of *T. lanuginosus* and *Scytalidium thermophilum* (Yang et al. 2020) showed the presence of 23 metabolites from *T. lanuginosus*. Among these, there was also a new metabolite, therlanubutanolide, and 15 known compounds. In addition, seven known compounds were obtained from *S. thermophilum*. Also, a polyketide synthase pathway-derived metabolite, three 3,4-dihydronaphthalen-1 (2H)-ones, was obtained from both fungi. This metabolite has been shown to possess antimicrobial activity and is known to be a phytotoxin in plant pathogenic fungi.

Nematicidal compounds have been described from a thermophilic fungus, belonging to a class of PKS-NRPS hybrid metabolites (Guo et al. 2012). These compounds from *Talaromyces thermophilus* were found to have a 13-membered lactam-bearing macrolactone, namely, thermolides A–F, as per NMR spectra. Two compounds showed nematicidal activity against three destructive nematodes: *Meloidogyne incognita, Bursaphelenches siyophilus*, and *Panagrellus redivevus.*

It is interesting to see that thermophilic fungi can not only synthesize bioactive metabolites but also facilitate biotransformation. Sreelatha et al. (2018) have shown that *T. lanuginosus* can convert spironolactone to the minor mammalian metabolites 7α-thiospironolactone (M1) canrenone (M2), 7α-thiomethylspironolactone (M3), and 6β-OH-7α-thiomethylspironolactone (M4). Hence, possessing similar mammalian enzyme systems, their potential in biotransformation, and production of important metabolites warrants exploration.

These thermophilic fungi can also be utilized for metabolic engineering as evidenced by the work of Li et al. (2020). They used the cellulolytic thermophilic filamentous fungus *Myceliophthora thermophile* in an attempt to produce ethanol from glucose and cellobiose. They introduced the ScADH1 gene into the wild-type strain and found that ethanol production was increased when glucose was used as substrate. However, overexpression of a glucose transporter or cellodextrin transport system from *N. crassa* resulted in increased ethanol production. Transcriptomic analysis showed downregulation of genes involved in oxidation–reduction reactions and stress response but upregulation of protein synthesis related genes.

3.10 Conclusion

It is obvious from this chapter that thermophilic fungi hold great potential for future prospects in industry. While many such fungi have been isolated, identified, and sequenced, whole-genome sequences and the mining of information from their genes are yet to be comprehensively elucidated. Next-generation sequencing technologies are set to play a vital role in better understanding this unique group of fungi. Considering that metagenome analysis of thermophilic fungi, though very less, has shown matches with fungi already documented, this can ease out the process of information mining. It is expected that in the next few years, a wealth of information repository would be developed focusing on thermophilic fungi.

Acknowledgement Authors acknowledge Jaypee Institute of Information Technology, Noida for providing infrastructure.

Conflict of Interest Authors declare no conflict of interest.

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