

Chapter 3

Thermotolerance and Adaptation to Climate Change



Michel Almaguer Chávez

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Abbreviations

CYA Czapek Yeast Autolysate Agar
HSP Heat shock proteins

M. Almaguer Chávez (✉)
Faculty of Biology, University of Havana, Havana, Cuba
e-mail: michelalm@fbio.uh.cu

3.1 Introduction

Temperature is closely related to fungal biology, affecting various processes such as growth, reproduction, spore formation, germination, and indeed all activities of the organism (Paterson and Lima 2019). The values of environmental temperature allow fungi with limits outside a certain range of variation to be excluded. This occurs because the tolerable conditions do not allow it to develop or to complete its life cycle. This exclusion effect is immediate and determines the fungal populations that are present in certain habitats. There may also be a less immediate effect whereby this environmental factor may have a selective effect among fungi whose development ranges are within the ambient temperature range. In this way, fungi whose optimum temperatures are close to the prevailing temperature will be the most favored (de Menezes et al. 2019). In this way, this environmental factor affects the ecology of fungi.

Each fungal species has a growth rate to a certain temperature, and hence cardinal temperatures have been identified. These are the minimum temperature where growth occurs, the optimum temperature where optimal growth occurs, and the maximum temperature at which it can grow (Fig. 3.1). In the temperature-growth rate curve, there is characteristically a linear portion in which growth increases directly with temperature, an optimum range that may be narrow or rather broad, and a descending limb as the temperature becomes too high for growth (Cochrane 1958).

According to the response to this environmental factor, fungi have been classified as psychrophilic, mesophilic, thermotolerant, and thermophilic (Fig. 3.2). There are divergences in the grouping and classification of some species because it is

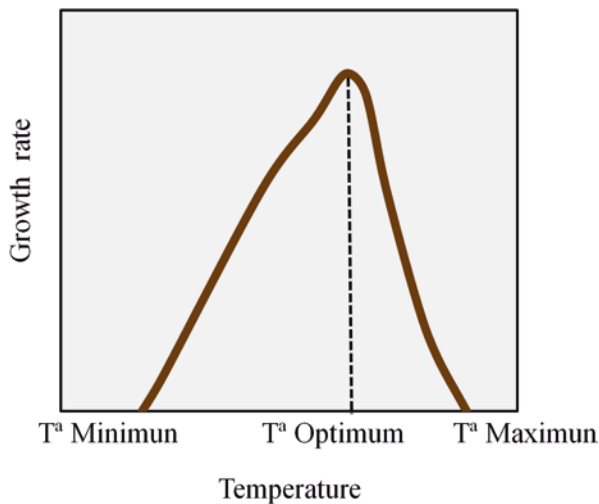


Fig. 3.1 Typical curve of growth as a function of temperature. Minimum, optimum, and maximum temperature where growth occurs

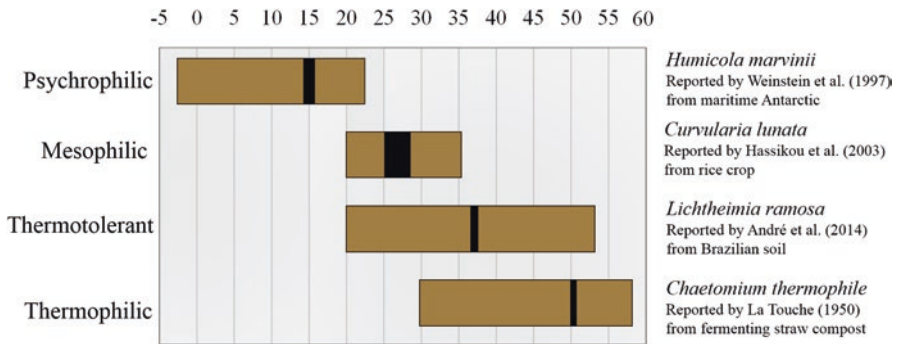


Fig. 3.2 Temperature ranges for the growth of some psychrophilic, mesophilic, thermotolerant, and thermophilic fungal species. ■ Optimum temperature range, ■ temperature range of fungal growth

difficult to specify precisely the limits in each group. However, this classification helps to understand the relationship of fungal growth with this environmental factor. There is evidence that in the same species there may be a variable range of response, which shows certain diversity (Rangel et al. 2005).

Few fungi are psychrophilic or psychrotolerant, with the ability to survive but not to grow at temperatures below 5 °C (Fig. 3.2). Such is the case of *Humicola marvinii* reported by Weinstein et al. (1997) on Signy Island, Antarctic. In this group, the term psychrophilic has also been proposed, for those organisms that have an optimum growth at temperatures not higher than 16 °C and a maximum at around 20 °C (Morris and Clarke 1987). Most of the known fungi are mesophilic and can develop between 10 and 35 °C, with optimum growth temperature between 20 and 30 °C (Cooney and Emerson 1964). Hassikou et al. (2003) reported the mesophilic growth rates of a *Curvularia lunata* strain isolated from a rice crop. Relatively few fungi can grow at temperatures above 37 °C, and it is suggested that the upper limit for the growth of any fungus is approximately 62 °C. This group of fungi that can grow at high temperatures is thermophilic, with minimum growth of about 20 °C, optimal development in the range of 40 to 50 °C, and a maximum of up to 50 °C or more. For example, some hyphomycetes isolated from hot springs by Tansey (1973) had a maximum growth temperature of 61.5 °C (Brown and Fritz 2019). Such is the case of *Chaetomium thermophile* reported by La Touche (1950) from fermenting straw compost. Fungi, being eukaryotic organisms, are much more sensitive than other domains of life (*Archaea* and *Bacteria*), and at temperatures above 65 °C, their membranes become more sensitive or can be irreparably damaged. However, since the investigations of Cooney and Emerson (1964), several fungi that can develop at high temperatures have been described. The information on the taxonomy, physiological characteristics, and ecology of these fungi capable of surviving under high temperatures has been provided (Maheshwari et al. 2000).

There are mesophilic fungi that may have the ability to survive or maintain viability at high temperatures and are classified as thermotolerant. Such is the case of

Lichtheimia ramosa reported by André et al. (2014) from Brazilian soil (Fig. 3.2). This group is distinguished from those with the true ability to actively grow as a thermophilic at high temperatures (Magan 2007). Thermophilic and thermotolerant fungal species are distinguished based on their minimum and maximum growth temperature (Fig. 3.2). Thermophilic fungi have a minimum growth temperature of 20 °C or higher and a maximum growth temperature of 50 °C or higher. However, thermotolerant have a wider growth temperature range, ranging from less than 20 °C to about 55 °C (Cooney and Emerson 1964; Maheshwari et al. 2000). Thermotolerant species can often be part of fungal communities that colonize a variety of humid organic substrates and where temperatures can be high. These substrates include hay, straw or cereal-based fertilizers, bird nests, and tropical soils (Magan 2007).

Evans (1971) studied more than 30 species isolated from coal spoil tips and delineated the differences between thermophilic and thermotolerant, according to their growth at various temperatures. The aforementioned study argued that the definition of Cooney and Emerson (1964) was becoming artificial and obscure, delimiting heat-tolerant fungi into three groups. Group 1 (strong thermophilic) constitutes the obligate thermophilic, while Group 2 (weak thermophilic) and Group 3 (strong thermotolerant) species form a transition stage between true thermophilia and general thermotolerance. This last term covers the species included in Group 4 (thermotolerant in general). Then it was suggested that the strains of certain fungi were transitional between the thermophilic and thermotolerant groups (de Oliveira and Rodrigues 2019). In this sense, a thermotolerant fungus could grow at 45 °C or higher, usually with a maximum close to 50 °C, but it can also grow below 20 °C. Another important contribution from Evans (1971) is the identification of two broad groupings within thermotolerant. In one group were strong thermotolerant fungi that grew well at 50 °C and often up to 55 °C. However, they grew little at temperatures below 20 °C, with a minimum growth temperature close to this temperature. Due to this behavior, he did not consider them to be true thermophilic (Fig. 3.3). The other group was generally termed thermotolerant, as they grew well over a wide temperature range. Species in this group had their optimum at around 40 °C, were able to grow at temperatures well below 20 °C, and mostly grew very slowly or not at all above 50 °C.

The thermotolerance of some fungal species may also allow a less immediate exclusion effect in the face of an increase in this environmental factor, with ecological implications. In nature, the temperature fluctuates intraday (i.e., day and night), between seasons (i.e., spring, summer, autumn, winter, dry period-rainy period), and even between long-time series (Roy and Bhattacharya 2020). This contributes to the fact that habitat conditions are generally not always optimal for the same fungal population and is related to cyclical patterns of species succession in communities.

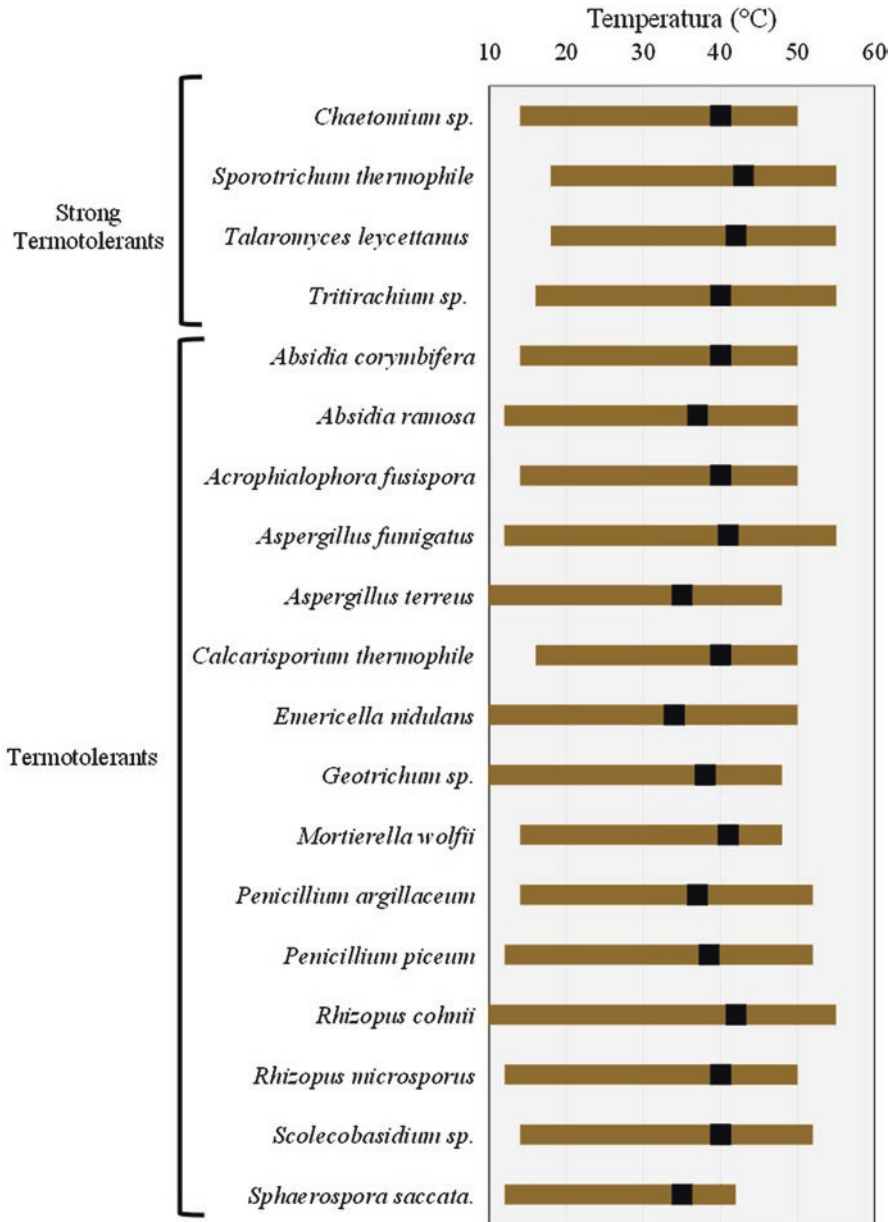


Fig. 3.3 Optimal, minimum, and maximum temperatures for the growth of some thermotolerant fungi. ■ Optimal temperatures, ■ minimum and maximum temperatures (Data from Evans 1971)

3.2 Mechanisms of Fungal Thermotolerance

Temperature can exert a marked influence on all aspects of fungal development, and various cellular processes contribute to the tolerance of different fungi to wide ranges of this abiotic factor. Joshi et al. (2020) based on what was argued by Grime (1977) suggest that fungi use strategies to survive and thrive in different environments. This is based on evidence for the existence of three primary strategies and their relevance to ecological and evolutionary theory. These three primary strategies can be competitive, stressful, and rude, but there may even be secondary strategies in combination. Competitive strategies are used when conditions are not stressful and maximize the exploitation of resources. Competitive characteristics are evident in fungi such as *Armillaria mellea* and *Serpula lacrymans*, which are responsible for long-term infections of timber and produce a consolidated mycelium which may extend rapidly through the production of rhizomorphs. Stress strategies involve adaptation to ongoing stress. Examples of stress-tolerant fungi appear to include the slow-growing basidiomycetes, which form the terminal stages of fungal succession on decaying matter, and the various fungi that occur in lichens and ectotrophic mycorrhizas. All of the stress-tolerant fungi are characterized by slow-growing, relatively persistent mycelia and low reproductive effort. Ruderal strategies are used under conditions rich in nutrients drastically disturbed by reducing their availability and increasing the reproductive potential of the fungus. Ruderal lifestyles are particularly characteristic of the mucorales, in which most species are ephemeral colonists of organic substrates. These fungi grow exceedingly rapidly and exploit the initial abundance of sugars, but as the supply of soluble carbohydrate declines, they cease mycelial growth and sporulate profusely.

The optimum temperature for growth is usually defined as the temperature at which the growth rate is maximum. This phenotypic character is related to the occurrence and velocity of various cellular and biochemical processes involved in growth. The involvement of these mechanisms has also been hypothesized to explain the basis for thermophilia and thermotolerance (Crisan 1973; Magan 2007). These cellular and biochemical processes include lipid solubilization, rapid resynthesis of essential metabolites, molecular thermostability, and ultrastructural thermostability.

Structural thermostability is of vital importance since there is the possibility that solubilization of cellular lipids occurs at high temperatures, with the danger that the cells lose their integrity. An increase in temperature can result in cellular lipids that contain more saturated fatty acids that have a higher melting point than those present in most mesophilic that do not show thermotolerance and that contain markedly less saturated lipids. Therefore, this characteristic contributes to maintain cell integrity at higher temperatures than in the case of mesophilic. It has also been suggested that increased fluidity of saturated lipids at high temperatures may enable metabolic activity and cell function to allow active growth at temperatures above 40 °C (Magan 2007).

Several investigations have focused on the ability of various fungi to produce heat shock proteins (HSP) when exposed to extreme temperatures (Tiwari et al. 2015; Wang et al. 2020). In heat shock, HSPs perform the equally important but different function of molecular chaperones. They participate in the stabilization of proteins and the adaptive modification of the composition of cellular proteins. This includes the identification of defective proteins, their partial proteolysis and refolding, as well as the control of the folding of newly synthesized polypeptides. However, the work on fungal HSPs is less than on other organisms. The studies carried out in *Aspergillus nidulans*, *Neurospora crassa*, *Saccharomyces cerevisiae*, and *Schizophyllum commune* stand out (Ewaze et al. 2007; Higgins and Lilly 1993; Newbury and Peberdy 1996). In most of the referred cases, the studies have involved the exposure of strains of these species to temperatures between 45 and 55 °C. Such conditions have been found to reduce the growth but not the development of aerial hyphae and often result in the appearance of various proteins that are rapidly synthesized or increased. In the basidiomycete *Schizophyllum commune*, proteolytic processes were also found to be significantly affected by such exposure (Higgins and Lilly 1993; Magan 2007). Different fungal HSPs related to thermotolerance were reviewed by Tiwari et al. (2015) based on their molecular weight, cellular localization, and functional characterization. Mainly expression of Hsp10, Hsp30, Hsp60, Hsp90, and Hsp104 increased in fungi exposed to heat stress (Table 3.1).

Fungi exposed to nonlethal heat shock can acquire resistance to lethal heat shock and then turn on acquired thermotolerant (Tereshina 2005). Piper (1993) reported molecular events associated with the acquisition of heat tolerance by the yeast *Saccharomyces cerevisiae*. Cells of this yeast that grow optimally at 25 °C acquire resistance to a lethal temperature of 50 °C when exposed to a temperature of 37 °C.

Maheshwari et al. (2000) reported acquired thermotolerance in mesophilic species, related to a greater survival at a lethal temperature, after a brief exposure to sublethal temperatures. The nonlethal heat shock could be associated with some mechanisms: synthesis of HSPs, synthesis of trehalose (up to 0.5 M), maintenance of intracellular pH through regulation of membrane ATPase activity, a decrease in the water activity and/or its redistribution in cytosol compartments, and detoxification of reactive oxygen species (Piper 1993; Tereshina 2005; Wang et al. 2020).

Attention has been more frequently focused on HSPs, which can be synthesized at high levels in response to brief exposure (i.e., 1 h) to high temperatures, such as 45–55 °C (Deacon 2013). HSPs are ubiquitous, present both under normal conditions and at elevated temperatures, and act as chaperones, ensuring that the cellular proteins fold correctly and that damaged proteins are destroyed. Maheshwari et al. (2000) stated that the synthesis of HSPs is an adaptive response to increased thermotolerance and survival in stressful conditions. Trent et al. (1994) observed that conidia of *Thermomyces lanuginosus*, germinated at 50 °C and subjected to heat shock at 55 °C for 60 min before exposure to 58 °C, showed greater survival compared to non-shocked conidia thermal. The experimental evidence they obtained allowed them to detect an increase in the synthesis of eight HSPs at 55 °C (Maheshwari et al. 2000; Magan 2007). Guimaraes et al. (2011), Iyalla (2017), and Zhang and Xu (2018) reported that a transient synthesis of HSP60 was involved in

Table 3.1 Some fungal heat shock proteins related to thermotolerance

HSPs	Cellular location	Fungi	References
HSP10	Mitochondria	<i>Saccharomyces cerevisiae</i> <i>Aureobasidium melanogenum</i>	Ricke and Bielsky (2006), Tiwari et al. (2015), Jia et al. (2018)
HSP12	Cytoplasm, cell wall, plasma membrane	<i>Saccharomyces cerevisiae</i>	Varela et al. (1995), Welker et al. (2010), Tiwari et al. (2015)
HSP30	Plasma membrane	<i>Saccharomyces cerevisiae</i>	Amoros and Estruch (2001), Tiwari et al. (2015)
HSP40	Cytosol, mitochondria, endoplasmic reticulum	<i>Lentinula edodes</i>	Hartl and Hayer-Hartl (2002), Fan et al. (2003), Tiwari et al. (2015)
HSP42	Cytosol	<i>Aspergillus fumigatus</i>	Haslbeck et al. (2004), Ghazaei (2017), Tiwari et al. (2015)
HSP60	Mitochondria, cytosol	<i>Penicillium marneffei</i>	Chandler et al. (2008), Cappello et al. (2009), Tiwari et al. (2015), Bakar et al. (2020)
HSP70	Cytosol, nucleus, endoplasmic reticulum, ribosomes, mitochondria	<i>Vairimorpha necatrix</i> <i>Trichoderma</i> sp. <i>Candida albicans</i>	Hirt et al. (1997), Montero-Barrientos et al. (2008), Leach et al. (2012), Tiwari et al. (2015)
HSP78	Mitochondria	<i>Vairimorpha necatrix</i>	Hirt et al. (1997), Tiwari et al. (2015)
HSP90	Cytosol, endoplasmic reticulum, nucleus	<i>Saccharomyces cerevisiae</i> <i>Candida albicans</i>	Sorger (1991), Leach et al. (2012), Tiwari et al. (2015), O'Meara et al. (2017)
HSP104	Cytosol	<i>Saccharomyces cerevisiae</i> <i>Cryptococcus neoformans</i>	Boreham and Mitchel (1994), Glover and Lindquist (1998), Tiwari et al. (2015), Yang et al. (2017)

the development of *Histoplasma capsulatum* and orchestrates the adaptation to high-temperature stress. Advances in the sequences of the complete genome of thermotolerant fungi will make it possible to examine the physiological pathways involved and the number of genes that regulate their production, which will allow a more complete understanding of the groups of genes involved in this process and therefore in thermophilia or thermotolerance.

In addition to the function of HSPs at elevated temperatures, the concomitant production of polyhydric alcohols (polyols) has also been detected (Magan 2007; Maheshwari et al. 2000). Polyols (i.e., glycerol and mannitol) also tend to accumulate in response to stress conditions. Heat stabilizing factors in the cytosol can also contribute to the thermostability of enzymes (Deacon 2013).

It is also suggested that trehalose acts as a general protector against stress in the cytosol and stabilizes the membranes during dehydration. Tereshina (2005) stated that the parallel synthesis of HSPs and trehalose occurs in response to heat shock and is related to the acquisition of thermotolerance by fungal cells.

Among the roles of trehalose are to reserve carbohydrate used during germination and in the storage process of fungal spores, membrane protector under various types of stress (thermal, oxidative, and osmotic stresses and stresses caused by heavy metals, drugs, and metabolic inhibitors), regulator of the glycolysis process and the cellular concentrations of glucose and ATP, and chemical chaperone involved in the stabilization and folding of proteins.

Trehalose synthetase and trehalase, the enzymes involved in trehalose metabolism, may well be attributed to HSPs. The roles of HSPs and trehalose in the acquisition of thermotolerance can vary, depending on the stage of development and the rate of protein synthesis related to it (Liu et al. 2019). In the spores, which are more thermotolerant latent structures, HSPs were not revealed since protein synthesis is absent. However, accumulation of trehalose is observed. The thermoprotective function of trehalose is related to the characteristic features of its structure and the ability to form intermolecular hydrogen bonds, which contribute to stabilizing proteins and membranes. In addition, it performs protective and chaperone functions, as well as a regulatory function by controlling the evolution of glucose in glycolysis and the activity of membrane-associated ATPase (Wang et al. 2020). The other aspect of the thermoprotective function of trehalose is related to the specific characteristics of the regulation of trehalose synthesis by the induction of the expression of the trehalose synthetase gene under heat shock, as well as by the direct activation of this enzyme by the rise in temperature. Thus, trehalose acts both in emergencies and in the long-term protection of subcellular structures during exposure to stressors, participating, together with molecular companions, in a unified process of protection against stress and quality control of proteins (Paixão et al. 2019; Tereshina 2005).

High temperatures are a problem in many biological systems, particularly those involved in complex macromolecular assemblages such as ribosomes. This relationship between thermotolerance, the virulence of a pathogenic fungus, and ribosome biogenesis have been observed in *A. fumigatus*, which may offer new avenues for the development of new antifungals that disrupt thermotolerant ribosome assemblage (Bhabhra and Askew 2005).

Fungi that can grow in desertification conditions are exposed to a wide temperature range that can have an action of thermostable enzymes (Joshi et al. 2020). For example, *Thermomyces lanuginosus* produces a large number of chitinases with greater stability against high temperatures (Khan et al. 2015). Ahirwar et al. (2017) isolated thermotolerant fungi producing hemicellulases from heated environments.

Melanin deposition on the cell wall can also influence thermotolerance and could be related to fungal geographical distribution and ecology (Cordero and Casadevall 2017). The ubiquitous presence of Ascomycota in soil samples worldwide is attributed to its highly competitive capacities together with the presence of melanin (Egidi et al. 2019; Lin and Xu 2020). Environmental factors have been shown to influence the deposition of melanin content in the membrane of strain XJ5-1 of the yeast *Aureobasidium melanogenum*, isolated from the desert (Jiang et al. 2016). In this particular example, the presence of melanin confers higher tolerance to heat treatment (40 °C), besides UV radiation, oxidation, salt shock, desiccation, and

strong acid hydrolysis at high temperature, for example, 80 °C (Lin and Xu 2020). Melanization increased tolerance to heat stress in *C. neoformans* and *Wangiella dermatitidis* (Cordero and Casadevall 2017). Joshi et al. (2020) compile several investigations that refer that melanin is also related to the adaptability of fungi in other hostile environments. Some current studies with melanotic fungi have revealed a wide spectrum of functions for this kind of pigment, ranging from drought and radiation resistance to increased virulence in fungal pathogens (Lin and Xu 2020). In *Monilinia fructicola*, melanin functions to provide the conidia with resistance to a variety of environmental stresses such as high temperatures (Rehnstrom and Free 1996; Cordero and Casadevall 2017). The role of melanin in fungal thermotolerance is scarce, that is why it is necessary to explore the various functions ascribed to this biological pigment in fungi and its relationship with climate change.

3.3 Spores, Resistance, and Survival

Temperature also influences the survival of various fungi, and this is related to the ability to form various structures that can be resistant to high temperatures. Most fungal propagules die on exposure to 80 °C for approximately 1 min. However, the ascospores of some food spoilage fungi such as *Neosartorya fischeri* can survive even for 1 h of exposure to temperatures around 85 °C (Baggerman and Samson 1988; Rajashekhara et al. 1998). In the investigation of Jesenska et al. (1993) with soil fungi, it was detected that the most heat-tolerant survived exposure to 90 °C for 1 h. For their part, the ascospores of *Byssochlamys fulva* and *Talaromyces macropora* are resistant to high temperatures and require heat activation for germination (Dijksterhuis et al. 2002).

Suryanarayanan et al. (2011) reported thermotolerance of mesophilic fungal spores that were common saprotrophs. They detected six ascomycetes, isolated from a semiarid tropical habitat subject to fire in India, which were able to grow after incubating their spores at 100 °C for 2 h in dry heat, in which two survived at 110 °C and one at 115 °C. Related to these results, they suggested the possibility that the form of constitutive heat tolerance expressed by fungi could represent a specific adaptation to prolonged periods of drought and the prevalence of fires in their dry habitat. This physiological trait may be widespread, putting a focus on the evolution of opportunistic pathogens on a warmer planet.

Some strains of entomopathogenic fungi such as *Beauveria* spp., *Isaria* spp. and *Metarhizium* spp. show an important survival of the conidia at high temperatures, with a relationship between the thermotolerance of the conidia and their origin from geographic isolation. Most entomopathogenic fungi are mesophilic and can develop between 10 and 40 °C, but optimal growth is between 25 and 35 °C. The temperature has the greatest impact on conidial stress that inhibits metabolic processes, such as decreased morphogenesis during germination, protein denaturation, and membrane disorganization. Thermal stress directly impacts the ability of fungal strains to

attack arthropods and their performance of an environmental activity (Paixão et al. 2019).

In spores, which are more thermotolerant latent structures, HSPs are not reported since protein synthesis is absent. However, accumulation of trehalose is observed with an important thermoprotective function previously analyzed (Paixão et al. 2019; Tereshina 2005).

3.4 Thermotolerance and Its Relationship with Environmental Changes

Ever since the basis of the thermotolerance studies, fungi in natural environments have provided abundant evidence that the active fungal community depends on thermal conditions (Carreiro and Koske 1992a, b, c; Widden 1986). Cochrane (1958) suggested that subtropical strains of a particular fungus may have higher optimal growth temperatures than strains from temperate regions. Therefore, isolates of the same species from different geographical areas may differ in their temperature-growth relationships. Later Evans (1971) concluded that the strains of certain fungi are transitional between thermotolerant and thermophilic, depending on environmental pressures. Thermotolerant fungal strains that grow in a habitat subjected to constant high temperatures can become dependent on these high temperatures for continued growth, and this could be a natural step in the evolution toward thermophilia. Evans (1971) also suggested that some thermotolerant species such as *Aspergillus fumigatus* can grow at lower temperatures and, therefore, will be able to compete with mesophilic populations. For their part, Craveri et al. (1964) stated that weak thermophilic species and strong thermotolerant species form a transition group between true thermophilia and general thermotolerance. Thermotolerant species grow in a wide temperature range, that is, they grow in the normal mesophilic range (10–35 °C) but can also grow up to 48–50 °C and occasionally more. These high growth temperatures can be important in determining the habitats in which thermotolerant fungi occur, and a versatile temperature range for growth will be especially important in environments subject to wide temperature fluctuations.

Maheshwari et al. (2000) analyzed the evolutionary pathways toward fungal thermotolerance. They argued that any new mutation in a fungal population would spread, ultimately replacing the wild type. The replacement rate will depend on your growth advantage, which in turn depends on selective pressure. De Crecy et al. (2009) observed that favorable variants take longer to prevail during certain cycles, which seems to indicate that evolution is occurring in discrete steps and that a different evolutionary path may encounter different thermal barriers.

For most organisms, growth occurs best in a relatively narrow temperature range and lags well outside this range (Huey and Stevenson 1979; McLean et al. 2005). Temperatures that allow for relatively rapid growth can vary between genotypes, and natural selection favor particular variants given spatial and temporal patterns of

environmental temperature. The theory of evolution of thermal reaction norms for yield, such as growth rate, is based on the assumptions that yield contributes additively to fitness and there is a trade-off between yields at different temperatures. Based on these assumptions, this theory predicts that thermal specialists will outperform thermal generalists in most patterns of environmental variation. A fundamental trade-off exists between specialists and generalists that results from specialization for environmental condition (Moor et al. 2020). The generalist species can survive in a wide variety of temperatures with different resources, while specialist species have narrower requirements and tolerances. According to Angilletta et al. (2010), generalists can perform over a wider range of temperatures but perform poorer than specialists at the optimum temperature. Therefore, organisms must tolerate a wide range of environmental conditions but restrict growth under specific environmental conditions. In fact, generalists are only expected to outperform specialists when the environmental temperature is relatively stable within generations but varies between generations (Gilchrist 1995).

It has been argued that the urbanization of our planet has created rapid changes in the climate. Air and ground temperatures have increased in urban areas compared to their surroundings, and this phenomenon is known as the urban heat island effect. Causes include both increased heat absorption by pavement and buildings and increased heat production by air-conditioners, traffic, and factories in urban areas. In general, urban heat islands are characterized by higher minimum, average, and maximum temperatures. Urban heat islands have been exerting evolutionary pressure on organisms for at least 50 years and for more than 100 years in some cities (Brazel et al. 2000; McLean et al. 2005; Tereschenko and Filonov 2001).

Given the gradual increase in temperatures that has been associated with urbanization, fungi have begun to adapt to the warmer conditions of urban soils. McLean et al. (2005) studied the thermal reaction norms (18–26 °C) for the growth rate of four species of chitinolytic fungi (*Chrysosporium pannorum*, *Penicillium bilaii*, *Torulomyces lagena*, and *Trichoderma koningii*) compared between urban and rural sites near Louisville, Kentucky. Urban isolates of *C. pannorum* and *T. koningii* grew faster than rural isolates at 26 °C but grew more slowly than rural isolates at 18 °C. This difference in the thermal reaction norms between urban and rural isolates allowed them to suggest that urbanization caused thermal specialization. In this process, natural selection was able to produce urban genotypes that grow faster than rural genotypes at high temperatures but slower than rural genotypes at low temperatures. On the other hand, urban isolates of *T. lagena* and *P. bilaii* grew as fast as or faster than rural isolates at all temperatures, suggesting that counter-gradient variation could also occur. In such variation against the gradient, natural selection could produce urban genotypes that grow faster than rural genotypes at all temperatures. Thermal adaptation of the fungi analyzed was similar to that observed in other ectothermic organisms where the fungal thallus temperature varies according to the environmental temperature where it is found (Angilletta et al. 2002, 2003; Conover and Schultz 1995; Huey and Kingsolver 1993; McLean et al. 2005).

The emergence of these patterns may be because the genetic structure of populations changes at the beginning of urbanization, causing different responses to

selection in each species. If there are no specialized genotypes for high-temperature growth within a population, selection for more optimal growth at high temperatures could produce a counter-gradient variation. Another possibility is that the specific biology of each species makes one form of adaptation more favorable than another (McLean et al. 2005). Thermal specialization and counter-gradient variation in growth rate involve different proximate mechanisms, which in turn lead to different evolutionary trade-offs (Angilletta et al. 2003). If the fitness consequences of these trade-offs vary between species, natural selection might favor thermal specialization in some species and counter-gradient variation in others. Unlike the first possible explanation, the latter does not imply genetic restrictions as the cause of the different patterns of intraspecific variation (McLean et al. 2005). Different responses to urbanization can disrupt competitive relationships between fungi, which can affect organic matter decomposition and nutrient cycling and trophic networks (Bonkowski et al. 2000; Carreiro and Koske 1992b; Marín et al. 1998; McLean et al. 2005; Naár and Kecskés 1998).

3.5 Habitats of Thermotolerant Fungi

Changes in climate can have impacts on fungal biodiversity patterns. Variation in thermal reaction norms could have broader impacts on the dynamics of communities in urban settings and the processes of the ecosystems that contain those communities (McLean et al. 2005).

Thermotolerant fungi represent a heterogeneous group made up of a large number of morphological and physiological forms with variability in their adaptation to high temperatures and therefore to climatic variations (Narayan and Prakash 2019). The habitat of thermotolerant fungi ranges from the hot natural environments to artificial environments (Fig. 3.4). Several investigations reported a wide range of these organisms causing spoilage of bagasse, grains, groundnut, hay, palm kernels, peat, wood chips, and other agricultural crops. These fungi are also detected in animal and industrial wastes and processes related to the biodegradation of lignocellulose.

Several investigations reported the detection of thermotolerant fungi in soils with high temperatures. The results of Murgia et al. (2019) showed high biodiversity in the desert sand of the Middle East, consisting predominantly of fungi that have adapted to survive in the extreme environmental conditions that prevail in deserts, indicating the resistance of fungi of the Dothideomycetes classes, Pezizomycetes, and Sordariomycetes, such as *Albifimbria terrestris*, *Fusarium equiseti*, *F. redolens*, *F. solani*, and *Chaetomium madrasense*. The presence of these fungi in the soil may be related to the solar heating they receive (Saroj et al. 2017), and this may determine that the fungi present in that habitat can grow at temperatures above 50 °C or even have viability at 80 °C (Joshi et al. 2020). Rajavaram et al. (2010) made soil isolates from mines, animal manures, cattle dung, composts, industrial wastes, poultry manure, and vermicompost and found *Aspergillus fumigatus* in all

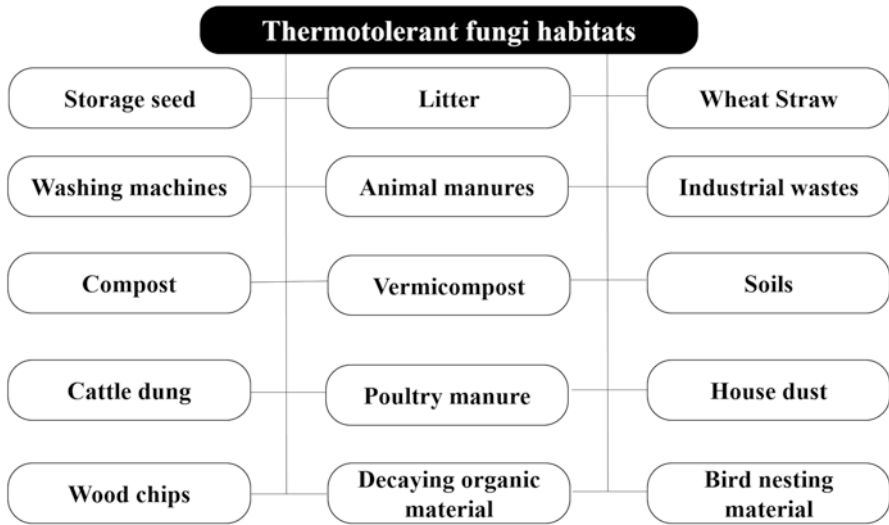


Fig. 3.4 Wide range habitats of thermotolerant fungi ranging from hot natural environment to artificial environments

substrates. Salar and Aneja (2006) found six species of thermotolerant fungi in temperate soils of northern India (*Aspergillus fumigatus*, *Chaetomium senegalense*, *Chrysosporium tropicum*, *Emericella nidulans*, *Penicillium chrysogenum*, and *Rhizopus microsporus*). Singh and Sandhu (1986) isolated thermotolerant strains of *A. aculeatus*, *A. carneus*, *A. fischeri*, *A. flavus*, and *A. nidulans* in soils of Port Blair.

Industrialization and the development of technologies have made possible the design, commercialization, and distribution of equipment that can reach temperatures higher than ambient temperatures, and consequently, new habitats have emerged for fungal populations. In this sense, washing machines and dishwashers can be considered extreme environments due to the high temperatures from which thermotolerant fungi have also been isolated (Zalar et al. 2011). Tischner et al. (2019) reported that 32% of the sampled washers in Hungary were highly contaminated with various species of fungi and 46% by human opportunistic pathogenic species. None of the fungi examined could grow at temperatures above 50 °C, so they can be considered thermotolerant species. Babic et al. (2015) hypothesized that washing machines could act as reservoirs for thermotolerant contaminating or pathogenic fungi.

Changes in climate and those expected in the coming decades are expected to have an impact on fungal biodiversity patterns, which, in turn, may also have implications for public health. Therefore, it is of vital importance to evaluate the ecological responses of fungi (Damialis et al. 2019).

Climate change is positive for all biomes but its effect increases moderately with latitude (Seidl et al. 2017). The studies conducted by Hoegh-Guldberg et al. (2019) show that climate warming of 1.5–2 °C is predicted to reduce permafrost in cold regions by 28–53%, resulting in large deposits of carbon available for microbial respiration and the emission of greenhouse gases that could lead to local extinction of cold-adapted fungi (Joshi et al. 2020). Gomes et al. (2018) reported diversity in Antarctic soils by identifying 218 fungi belonging to 22 taxa of 15 different genera belonging to the *Zygomycota*, *Ascomycota*, and *Basidiomycota* divisions. The genera *Antarctomyces*, *Mortierella*, *Penicillium*, and *Pseudogymnoascus* were the most frequently isolated, and *P. tardochrysogenum*, *P. verrucosus*, *Goffeauzyma gilvescens*, and *Mortierella* sp. were the most abundant taxa. Common yeasts in Antarctic soil belong to the genera *Candida*, *Cryptococcus*, *Debaryomyces*, *Guehomyces*, *Leucosporidiella*, *Metschnikowia*, and *Rhodotorula* (Martinez et al. 2016). Among these, there are genera with a wide distribution also in tropical areas. Further research directed toward the change in the stoichiometry (carbon/nitrogen ratio) of the soil of the polar region related to the changing climatic conditions would be a key step to predict the adverse effects on fungal communities (Alves et al. 2019).

Gange et al. (2007) reported rapid and recent changes in fungal fruiting patterns analyzing information on over 300 autumnal fruiting species, from more than a thousand zones, located in Southern England during 45 years (1950–2005). This study concludes that climate warming appears to have caused significant numbers of species to begin fruiting in spring as well as autumn. Until the time of the aforementioned study, several investigations had found recent phenological responses to climate change in higher organisms, such as plants, insects, or birds, and were restricted to events in spring (Parmesan and Yohe 2003; Toljander et al. 2006). Later Gange et al. (2011) informed about the relationship between climate change and host shifts in fungi and concluded that changing temperature causes altered growth rates, germination rates, and combative ability of one fungal species relative to another. Specifically, the case of *Auricularia auricula-judae* may have resulted in the ability to colonize a wider host range. The mean autumn fruiting period is nowadays later for saprotrophic and mycorrhizal fungi in Norway (Kausserud et al. 2008) and Switzerland (Büntgen et al. 2011). Moore et al. (2008) reported that since 1975, many species of fleshy fungi that previously fruited principally in autumn in the United Kingdom now also fruit during spring. Meanwhile, Kausserud et al. (2010) described spring fruiting nowadays occurs earlier than it did in the past century. According to Kausserud et al. (2008), these recent changes in fruiting are dependent on fungus life-history strategy, with variances between early fruiting species and late fruiting species. Kausserud et al. (2012) reported the temporal changes in the timing of fruit body formation to occur in all these European countries but are particularly pronounced in the United Kingdom, and it is related to geographical and bioclimatological features.

3.6 Thermotolerance within the Environmental Fungi

Thermotolerant fungi compose the mycobiota that grows in piled masses of plant material, heaps of agricultural and forestry products, stored food grains, and other accumulations of organic matter. In these ecosystems, the warm, humid, and aerobic environment provide the basic conditions for their development, and the fungal spores could become airborne from these native sources. For example, Narayan and Prakash (2019) reported 27 species of airborne thermotolerant fungi in India, from some of the aforementioned substrates, and highlighted *Aspergillus versicolor* and *Paecilomyces variotii*.

Studies on the thermotolerant airborne fungi are not as much of those carried out in other ecosystems. However, the relationship to air temperature and climate has been reported. Earlier and longer fungal sporulation seasons have been reported in the United Kingdom (Gange et al. 2007), Norway (Kausrud et al. 2012), and other European countries (Kasprzyk et al. 2016). Damialis et al. (2015a, b) demonstrated the beginning of a long-term trend in airborne spore concentrations in Thessaloniki during 1987–2005. Helfer (2014) showed that some fungal populations could be vulnerable to global environmental change. The sporulation and the formation of reproductive bodies of fungi are influenced by meteorological factors, such as rainfall, air temperature, and relative humidity (Carlile et al. 2001; Senanayake et al. 2020). Therefore, the variability in different stages of reproduction could cause modifications in the diversity of fungi and the temporal dynamics of the dispersion of their propagules. There is evidence that changing climate might cause alterations in phenology (Corden et al. 2003; Gange et al. 2007; Kausrud et al. 2012) and the dynamics of fungal communities (Gange et al. 2011).

Martínez-Herrera et al. (2016) reported that the ability to grow at temperatures of 55 °C and survive at 75 °C distinguished species in environmental strains of *Aspergillus* section *Fumigati* and allows the organisms to grow in decomposing organic matter and infect host mammals. *Aspergillus fumigatus* is particularly common, found in a wide range of environments, growing between 12 and 55 °C. However, it is considered more thermotolerant than thermophilic, because it can grow at temperatures as low as 12 °C and its optimal temperature is below 40 °C. This fungus is extraordinary for its wide growth temperature range and its equally varied range of habitats. It commonly grows in compost, substrates in indoor environments, moldy grains, and other decaying organic matter. It can also develop on the hydrocarbons of aviation fuel. In recent years, *A. fumigatus* has become a major problem in operating rooms, especially transplant units, because it can colonize wounds and grow within the tissues of transplant patients. However, it is an essentially saprotrophic species (Deacon 2013).

In *Aspergillus* section *Nigri*, the growth and conidia maturation occur more rapidly at temperatures between 28 and 30 °C (Marín et al. 1998). *Aspergillus niger* is a mesophilic species (Belli et al. 2004). However, Rojas et al. (2010) found that some environmental strains, isolated from Cuba, grew from 18 to 40 °C in Czapek Yeast Autolysate Agar (CYA) medium. However, Rojas et al. (2010) surprisingly

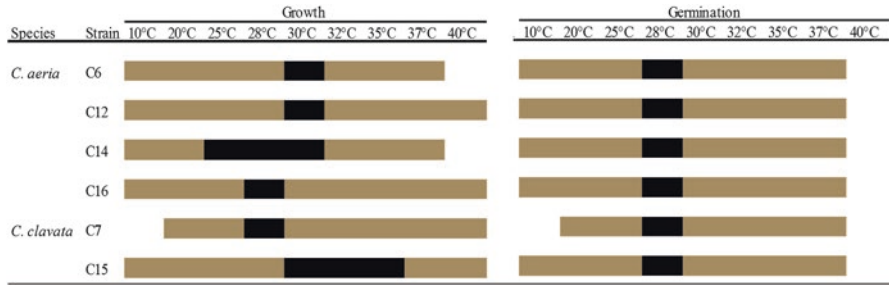


Fig. 3.5 Growth and conidia germination of *C. aerea* and *C. clavata* strains at different temperatures. Fungal strains were isolated from the atmosphere of a rice agroecosystem in Cuba

found the presence of several strains with optimal growth between 28 and 37 °C. In general, black aspergilli are less thermotolerant than *Aspergillus* section *Fumigati*, which perhaps leads to the fact that the majority of nosocomial cases of aspergillosis are caused mainly by *A. fumigatus* and not by *A. niger* (Scazzocchio 2009).

Other thermotolerant fungi have been detected in some investigations concerning the physiology of environmental fungal strains. A growth study, from 10 to 40 °C with mesophilic strains of *Curvularia* isolated from the atmosphere of a rice agroecosystem in Cuba, determined that two strains of *C. aerea* and two of *C. clavata* grew at 40 °C (Almaguer et al. 2013). Besides, conidia germination was observed between 10 and 37 °C (Fig. 3.5). In the aforementioned study, the differences between some strains show that the physiological behavior of each strain of the same species can differ considerably as a function of the moment of collection, the characteristics of the ecosystem, and the source of the inoculum.

Higher concentrations of airborne spores could be expected in tropical climates, where these temperature values are common throughout the year. Garcia-Solache and Casadevall (2010) warned about the potential risks of the adaptation of fungi to high temperatures and the importance of studying the possible effects of global warming on fungal populations since a warmer climate could change the distribution of species and favor those that are more thermotolerant. Additionally, under strong selection pressure, the prevalence of species adapted to heat tolerance may increase. In this sense, it has been shown that in urban areas, some fungi grow faster at high temperatures than in rural environments, and an increase in temperature can influence higher growth and an increase in the production of spores in *C. cladosporioides* (Damialis et al. 2015a, b). Sánchez and Almaguer (2018) confirmed the formation of conidia within the 10–34 °C interval and optimal growth in 25–30 °C, in environmental isolates of *Cladosporium cladosporioides*, collected from the atmosphere of Havana, Cuba. It was also observed that the isolates could be divided into three groups according to their physiological response to temperatures. One group had lower growth, sporulation, and germination values, and they were related to the lower temperatures around the isolation date. The species that formed the other two groups were collected on days when the average temperature was higher.

In addition, the variability of the response at different temperatures among the airborne propagules in Cuba was also found for several isolates of *Pyricularia oryzae* from a rice agroecosystem (Almaguer-Chávez et al. 2019). In this investigation, the formation of four groups between strains of *P. oryzae* isolated at various times during a year was observed. All these findings in airborne thermotolerant fungi may be related to genetic plasticity and could influence the ability to adapt to different environmental conditions. In this sense, Huo et al. (2012) stated that warmer conditions could alter the distribution of species and the incidence of fungal diseases in crops of economic interest. Moreover, climate change brings the specter of new infectious diseases (Casadevall 2020).

3.7 Perspectives of Fungal Thermotolerance Studies

Climate change can affect the diversity of the structure of fungal communities, since the survival of species sensitive to high temperatures may be affected, while resistant species will grow excessively creating an overpopulation of habitats (Joshi et al. 2020; Moreno et al. 2013). The specialized functions carried out by fungi in the ecosystem could be affected, such as decomposition, pathogenesis, and symbiosis. These changes in community structure and fungal diversity affect the ecosystem (Joshi et al. 2020; Setälä and McLean 2004). Climate change affects the diversity, geographic distribution, and composition of fungal communities around the world, and virulent fungal species capable of withstanding climatic disturbances will replace weakened species (Joshi et al. 2020; Moreno et al. 2013). For example, Newsham et al. (2016) recorded an increase of approximately five fungal taxa per °C of temperature increase. The diversity of fungi is greater in warmer habitats, but the evolutionary and environmental factors that shape the biogeography of fungi are not fully understood. However, according to the meta-analysis by Vetrovsky et al. (2019), high altitudes support concentrated fungal diversity and indicate a narrow climate tolerance of mycorrhizal fungi compared to pathogenic fungi. The aforementioned authors assembled a large set of previously generated mycobiome data linked to specific geographic locations around the world and used this dataset to describe the distribution of fungi and look for correlations with different environmental factors, including the weather. That meta-study identified climate as an important driver of different aspects of fungal biogeography, including the global distribution of common fungi, as well as the composition and diversity of fungal communities. The diversity of fungi was concentrated at high latitudes, in contrast to the opposite pattern shown previously for plants and other organisms. Mycorrhizal fungi appear to have closer climatic tolerances than pathogenic fungi. Then Vetrovsky et al. (2019) speculate that climate change could affect the functioning of the ecosystem due to the close climatic tolerances of the main fungal taxa.

The thermotolerance that is evidenced in several groups of environmental fungi has been related to the ability to grow in mammals and higher temperatures, and eventually global warming can exert pressure for the emergence of new diseases in

mammals. For this reason, there is a concern about new diseases caused by fungal agents (Garcia-Solache and Casadevall 2010).

According to Casadevall (2020), climate change brings the specter of new infectious diseases. The pillar of endothermy is robust in humans (37 °C), but it can be broken if fungi adapt to higher temperatures. Although most species of fungi cannot tolerate the temperatures of mammals, some species can adapt to survive higher temperatures by gradually being exposed to warmer temperatures. Thus, global warming will lead many fungal species to adapt to higher temperatures, and some with pathogenic potential for humans will break the thermal defensive barrier provided by endothermy (Robert and Casadevall 2009).

Fungi that are pathogenic to insects can be experimentally adapted to replicate at mammalian temperatures through progressive heating cycles, demonstrating that fungi can rapidly adapt to higher temperatures (Casadevall 2020; de Crecy et al. 2009). Rangel et al. (2005) reported variability in the conidial thermotolerance of *Metarhizium anisopliae*, isolated from different geographical origins. In general, isolates from higher latitudes demonstrated greater susceptibility to heat than isolates closer to the equator.

It has been suggested that in tropical and subtropical climates, thermotolerant fungi should be more abundant. Many fungal pathogens that are not found in temperate regions can be found in tropical regions, such as *Paracoccidioides brasiliensis*, *Penicillium marneffeii*, and *Cryptococcus gattii* (Casadevall 2020). The incidence of fungal infections in these locations tends to be higher, possibly due to increased numbers of fungi that can manage with human body temperatures. That is why the potential effects of global warming on fungi must be considered. Global warming could have a significant effect on fungal populations. First, a warmer climate could change the distribution of heat-tolerant and susceptible species by favoring those that are more thermotolerant and by creating the conditions for more environmental fungi to spread and come into closer contact with human populations. Second, under strong selective pressure, the prevalence of heat-tolerant species may increase (Raimalani and Pancharia 2020). Global warming means the narrowing of the thermal gradient between ambient temperature and that of mammals. The current gradient is approximately 22 °C, and consequently each degree of increase in global mean temperature reduces the gradient by approximately 5%. Casadevall et al. (2019) suggest that with current global warming, the prevalence of fungal diseases will increase. The risk of newly emerging fungal pathogens could be magnified by the fact that there are few antifungal medications available and there are no licensed vaccines.

The environment is likely to contain a large number of potentially pathogenic fungal species that are currently nonpathogenic to humans because they lack the ability to grow at the temperatures of mammals. The direct and indirect effects of climate changes induced by an exponentially growing human population as drivers of fungal evolution should be an area of intense investigation in the coming decades. The widening of the geographic range of innately pathogenic thermotolerant fungi and the acquisition of virulence traits in thermotolerant nonpathogenic environmental fungi may shape the twenty-first century as an era of expanding fungal diseases

(Casadevall et al. 2019). The recent appearance of *Candida auris* on three continents has been proposed to be related to global warming and the adaptations in certain microorganisms that make them pathogens for humans. This emergence evidences the need for increased surveillance and continuous monitoring (Casadevall 2020; Casadevall et al. 2019; Lockhart et al. 2017).

Global warming, strong climatic fluctuations, changes in rainfall patterns and drought, temperature changes, and forest fires are very evident in different parts of the world and affect fungal communities. Franco-Manchon et al. (2019) studied burned and unburned Scots pine forests, concluding that the dynamics of fungal communities were affected by forest fires. For example, mycorrhizal taxa were more affected than saprotrophic taxa by forest fires, as they were not observed the following year after forest fires. Nsa et al. (2020) isolated *Lichtheimia ramosa*, in a freshly burned field in Ikorodu, Nigeria. The genus *Lichtheimia* belongs to the class *Zygomycete* and includes saprotrophic species that can be isolated from decaying soil and plant material (Nagao et al. 2005). Its thermotolerance has been linked to its virulence (Alastruey-Izquierdo et al. 2010a; Schwartze et al. 2012; Schwartze and Jacobsen 2014). Attention to the thermotolerant genus *Lichtheimia* increased remarkably since its separation from the mesophilic genus *Absidia* and its taxonomic revision (Alastruey-Izquierdo et al. 2010b; André et al. 2014; Hoffmann et al. 2007; Hoffmann 2010). Ecologically, *L. ramosa* is abundant in soil, decaying plant debris, and food and is one of the causative agents of mucormycosis in humans (Nsa et al. 2020).

3.8 Climate Change and Aeromycological Dynamics

Fungi are adapting at a rapid rate in the face of environmental change. Joshi et al. (2020) reported that climate change caused an earlier and longer period of sporulation. Temperature is the environmental factor that systematically changes for decades and can significantly affect the growth and development of fungi, including the abundance of their sporulation (Kasprzyk et al. 2016). The concentration of airborne spores can increase in a wide range of temperatures as has been documented in countries around the world. In addition, the annual amounts of spores and their relationship with temperature were different between cities with climatic differences (Table 3.2).

Although the above examples explain the influence of temperature on the atmospheric dynamics of fungal propagules, it is not yet clear how medium- or long-term changes in climate, and particularly in temperature, affect the abundance of fungi in the air. Some investigations reported the probable impacts of climate change on airborne allergenic fungi and spore production (Barnes et al. 2013; Sindt et al. 2016). However, there is only limited evidence of trends in fungal development (Cecchi et al. 2010). Corden and Millington (2001) in Derby, UK, suggested a trend toward increasing annual counts of *Alternaria*, especially after 1992. Corden et al. (2003) reported that the abundance of *Alternaria* spores

Table 3.2 Some studies about relationships between temperature and airborne fungal spore concentration

Sampling period	Location	Fungi	Findings	References
2014–2015	Salamanca, España	<i>Alternaria</i>	Significant and positive correlation coefficients with temperature and total daily insolation	Fuentes et al. (2019)
2014–2016	Lisboa, Portugal	<i>Cladosporiumcladosporioides</i> , <i>Coprinus</i> , <i>Leptosphaeria</i> , <i>Agaricus</i> , <i>Cladosporium herbarum</i> , <i>Ustilago</i> , <i>Alternaria</i>	The mean temperature was the factor that exerted the greatest influence on the spore levels	Ferro et al. (2019)
2002–2014	Bratislava, Slovakia	<i>Alternaria</i> , <i>Epicoccum</i> , and <i>Stemphylium</i>	Considering that climate predictions for Central Europe indicate an increase in temperature events, shifts toward earlier onset, later end, longer duration, and increasing intensity of spore seasons of some fungal taxa in future years are expected, potentially exacerbating allergic respiratory disorders in humans	Ščevková et al. (2016)
1987–1996	Tulsa, Oklahoma	<i>Ganoderma</i>	Cumulative season total was significantly related to temperature	Craig and Levetin (2000)
2011–2014	SW of Iberian Peninsula	<i>Alternaria</i>	For a predicted increase in temperature in a climate change scenario, <i>Alternaria</i> spore production is foreseen to increase temperatures reaching optimal growing conditions in the two seasonal growing periods in Mediterranean climate	Maya-Manzano et al. (2016)

(continued)

Table 3.2 (continued)

Sampling period	Location	Fungi	Findings	References
2013	Szczecin, Poland	21 types of spores	The largest amount of the total variance in the spore composition was explained by the air temperature	Grinn-Gofrón et al. (2016)
2011–2012	Poland	<i>Cladosporium</i>	Warm and dry weather accelerate and elongate <i>Cladosporium</i> spore seasons in Poland	Kasprzyk et al. (2016)
2012–2013	Mexico City, Mexico	<i>Aspergillus</i>	Thermotolerance among <i>aspergillus</i> isolates from hospital environments	Martínez-Herrera et al. (2016)
2004–2013	Szczecin and Cracow, Poland	<i>Alternaria</i> and <i>Cladosporium</i>	As regards temperature, it was higher in Cracow and was still increasing in the studied years. If it increases, the peak value, total number of spores, and their average concentrations in a season will also increase	Grinn-Gofrón et al. (2016)
2003–2008	Madeira, Portugal	14 fungal genera	Temperature was the meteorological parameter that favored the most release and dispersal of the conidia	Sousa et al. (2016)
2003–2004	Taipei, China	Viable airborne fungi	Ambient temperature was the most consistent environmental factor positively correlated with fungal concentrations	Wu et al. (2007)

(continued)

Table 3.2 (continued)

Sampling period	Location	Fungi	Findings	References
1993–1996	Hualien, Taiwan	<i>Cladosporium</i> , <i>Arthrinium</i> / <i>Papularia</i> , <i>aspergillus</i> / <i>Penicillium</i> , <i>Ganoderma</i> , <i>Curvularia</i> , <i>fusarium</i> , <i>Ulocladium</i> / <i>Stemphylium</i> , <i>Cercospora</i> , <i>Alternaria</i> , <i>Drechslera</i> , <i>Torula</i> , <i>botrytis</i> , <i>Nigrospora</i> , <i>Pithomyces</i> , <i>Periconia</i> , ascospores, and other fungi	Among the meteorological factors, temperature was the most consistent predictor of fungal concentrations. Except for <i>aspergillus</i> / <i>Penicillium</i> and other fungi, higher temperature was positively associated with higher fungal levels	Ho et al. (2005)
2005	San Juan, Puerto Rico	Fungal spores	There were positive correlations between airborne fungal spore concentrations and temperature	Quintero and Rivera-Mariani (2010)
2001	Barbados	Fungal spores	Fungal spore concentration rose earlier in mid-July and remained so until October	Blades (2002)
2002	Medellín, Colombia	Fungal spores	Fungal spore concentration pollen levels in the atmosphere were associated with an increase or decrease in temperature	Angilletta et al. (2002)
1992–1995	Sydney, Australia	<i>Alternaria</i>	Fungal spore concentration pollen levels in the atmosphere were associated with an increase or decrease in temperature	Stennett and Beggs (2004)

(continued)

Table 3.2 (continued)

Sampling period	Location	Fungi	Findings	References
1980–1989	Stockholm, Sweden	<i>Cladosporium</i> and <i>Alternaria</i>	Daily mean temperatures of more than 15 °C when combined with a sufficient amount of precipitation seem to optimize the sporulation conditions for <i>Cladosporium</i>	Hjelmroos (1993)
1992	Waterloo, Canada	<i>Cladosporium</i> , <i>Epicoccum</i> , <i>Polythrincium</i> , <i>aspergillus</i> / <i>Penicillium</i> , <i>Leptosphaeria</i> , <i>Coprinus</i> , <i>Ganoderma</i>	The meteorological factors were, in descending order of importance, mean temperature, minimum temperature, and maximum temperature	Li and Kendrick (1995)
1991	Mexico City, Mexico	<i>Conidia</i> , <i>Basidiospores</i> , <i>Ascospores</i>	Daily mean spore concentrations were significantly correlated in southern and central areas with maximum temperature	Calderón et al. (1997)
1991–1993	Yokohama, Japan	<i>Cladosporium</i> , <i>Penicillium</i> , <i>Pestalotia</i> , <i>fusarium</i> , <i>aspergillus</i> , and others	The concentrations of fungi in outdoor air ($n = 288$) were significantly correlated with the maximum temperature of the day, minimum temperature of the day, average temperature of the day	Takahashi (1997)

(continued)

Table 3.2 (continued)

Sampling period	Location	Fungi	Findings	References
1997	Turin, Italy	<i>Cladosporium</i> , <i>Penicillium</i> , <i>Epicoccum</i> , <i>aspergillus</i> , and many others	Climatic and seasonal characteristics are prevalently determined by temperature; summer samplings are further forward on temperature gradient vector	Marchisio and Airaudi (2001)
1999–2000	Edirne, Turkey	<i>Cladosporium</i> , <i>aspergillus</i> , <i>Penicillium</i> , <i>Curvularia</i> , <i>Drechslera</i> , <i>Scytalidium</i> , <i>fusarium</i>	Temperature was the meteorological parameter correlated with spore levels	Asan et al. (2002)

varies greatly from one place to another depending on the regional vegetation and other local factors, among which temperature does not always play a determining role. Sindt et al. (2016) analyzed the temporal variations in a wide spectrum of characteristics of the atmospheric dynamics of *Cladosporium* in several French localities with different climatic conditions, with the aim of investigating the relationship between the levels of conidia and the evolution of the climate. On an annual basis and for 10 years, they demonstrated the climatic sensitivity of this fungal genus, the main component of the airborne fungi, and stated that the general increase in annual temperatures observed in recent years in several stations was consistent with those reported on warming. Regarding the potential impact of climate change, significant trends are identified by Hollins et al. (2004) when analyzing the relationships between airborne fungal spore concentration of *Cladosporium* and summer climate in Britain.

Hjelmroos (1993) suggested an upward linear trend in mean spore concentrations over time, in parallel with a positive trend in temperature. In Thessaloniki, Greece, a significant increase in air temperature has been observed during the period 1987–2005, and the annual mean concentrations of *Cladosporium* have decreased considerably and significantly between the years 1987 and 1992 and the years 1999 and 2005 (Damialis et al. 2015a), simulating different environmental regimes. Damialis et al. (2015b) have shown several fungi showed dramatic growth responses, with faster mycelium growth and lower spore production at higher temperatures. Several Spanish studies (Rodríguez-Rajo et al. 2005; Sabariego et al. 2000) demonstrated that average temperatures of 23–29 °C correspond to optimal conditions for high *Cladosporium* spore counts. Average temperature has been considered the most adequate predictor of its spore concentrations (Aira et al. 2012; Grinn-Gofroń et al. 2019; Hollins et al. 2004). For *Alternaria* (Thibaudon and Lachasse 2006), they stated that latitude had an undeniable impact on the concentration of spores. The majority of these works was conducted in temperate climates; however, the situation can be quite different in hot climates.

3.9 Conclusion and Future Prospects

Thermotolerance is present among fungi and could be essential for adaptation to climate change. Thermotolerance in fungi can be acquired in mesophilic species where environmental pressures exert selection on environmental mesophilic populations. Therefore, the gradual increase in temperatures, a consequence of climate change, proves to cause fungi to begin to adapt to warmer conditions and to change their ecological patterns. This incidence of changes in climate on fungal diversity may also have public health implications since fungal adaptation to survive at higher temperatures can undermine the pillar of endothermy. Therefore, it is of vital importance to evaluate the ecological responses of fungi to temperature.

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