



Fungal strategies for dealing with environment- and agriculture-induced stresses

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ABSTRACT

The Fungal Kingdom is responsible for many ecosystem services as well as many industrial and agricultural products. Nevertheless, how these fungal species function and carry out these services is dependent on their capacity to grow under different stress conditions caused by a variety of abiotic factors such as ionizing radiation, UV radiation, extremes of temperature, acidity and alkalinity, and environments of low nutritional status, low water activity, or polluted with, e.g. toxic metals or xenobiotics. This article reviews some natural or synthetic environments where fungi thrive under stress and have important impacts in agriculture and forestry.

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1. Introduction

Fungi are responsible for many industrial and agricultural products or processes as well as many ecosystem services (Alder-Rangel et al., 2018; Rangel et al., 2015a, 2015b). However, many of the environments where fungi provide these services or products are under extreme stress. For example, to produce ethanol, the yeast *Sacharomyces cerevisiae* needs to cope with high ethanol concentrations, oxidative and osmotic stress as well as high temperatures generated by fermentation (Eleutherio et al., 2015). Therefore, fungi must be able to respond adequately to the stress conditions to provide microbial services and products.

“Fungal stress” is a rather diffuse term (Ortiz-Urquiza and Keyhani, 2015). When is a fungal cell exposed to stress? Is every deviation from optimal growth in fact “stress”, and does the

terminology “suboptimal” imply that a cell is under stress? Alternatively, maximal (“optimal”) growth impinges on all metabolic pathways of the cell and stretches the physiology of the cell to its limits. One can imagine that even this state of a cell can be interpreted as stress.

The term “stress” in mycology refers to those situations that restrict or prevent the growth and reproduction of fungi. The classical language of biology has two expressions—namely *stimulus* to describe change in environment and *response* to describe the resulting change in the organism (Jennings, 1993). Classical heat shock response studies revealed two fundamental features: first, mild stress - which is the *stimulus* and second, the *response* which is the induction of a higher level of resistance (Hohmann and Mager, 2003; Rangel, 2011). This feature seems to be universal, and has even resulted as an “evolutionary Pavlovian conditioning response” for stresses that can be predicted (Mitchell et al., 2009). Environmental, cellular, and molecular aspects of stress effects and responses in yeasts and filamentous fungi have been reviewed by

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Avery et al. (2008). There is increasing awareness that stress may arise not only in natural systems subject or not to anthropogenic impact, but also under the comparatively controlled conditions of fungal culture.

2. Stressful environments in which fungi thrive

Fungi are ubiquitous components of the microbial communities of any terrestrial environment, including such hostile habitats as the Arctic, hot deserts, and metal-rich and hypersaline soils (Burford et al., 2003). Fungi are also ubiquitous in habitats polluted by xenobiotics, toxic metals and radionuclides, as well as leachates and other solid or liquid wastes (Fomina et al., 2005). Appreciation of fungi as agents of geochemical change is growing, and their significance is being discovered even in locations not usually regarded as prime fungal habitats, e.g. rocks, acid mine drainage, deep aquatic sediments, hydrothermal vents and the igneous oceanic crust (Gorbushina, 2007; Ivarsson et al., 2016; Reitner et al., 2006; Vázquez-Campos et al., 2014). In such habitats, fungi may exhibit a variety of mechanisms that determine tolerance and survival. These “extreme” locations may also act as a reservoir of novel organisms with unusual properties (Selbmann et al., 2013, 2017). Fungal strategies for dealing with environmental stress are interlinked with their ability to adopt a variety of growth, metabolic and morphological strategies, adaptive capabilities to environmental extremes and, their symbiotic associations with animals, plants, algae and cyanobacteria (Burford et al., 2003; Gadd, 2004; Selbmann et al., 2013).

2.1. Atmosphere

Fungi can be metabolically active in extreme habitats. One of the most extreme habitats in which fungi survive is the atmosphere, where low temperatures, low amounts of nutrients, extreme desiccation, and extreme ultraviolet radiation are found. Despite this, viable fungi have been isolated from aeroplanes (Holzapfel, 1978), stratospheric balloons (Harris et al., 2001), and rockets (Imshenetsky et al., 1976, 1977, 1978, 1979) from 10 to 50 km altitude in the stratosphere and 50–100 km above the Earth in the mesosphere (Christner, 2012; Imshenetsky et al., 1978). Fungi possessing black conidia (*Aspergillus niger*) and green conidia (*Penicillium notatum*) were collected from a rocket that reached the mesosphere at an altitude of 48–77 km (Imshenetsky et al., 1978). The fungus *Engyodontium album* was also collected from the stratosphere, at an altitude of 41 km (Wainwright et al., 2003). Since Antonie van Leeuwenhoek (van Leeuwenhoek, 1677) and Louis Pasteur (1860), microbes have usually been considered passive inhabitants of the atmosphere, dispersing via airborne dust particles. Present studies, however, reveal that bacteria and fungi are metabolically active even under those conditions (Amato, 2012; Amato et al., 2007), and that they act as a surface for the condensation of water vapor in the atmosphere, thus forming clouds (Christner, 2012; Christner et al., 2008; Delort et al., 2010). Fungi also serve as ice nuclei in clouds, which are required for snow and rainfall (Bowers et al., 2009; Delort et al., 2010; Frohlich-Nowoisky and Poschl, 2013; Richard et al., 1996). Fungal spores may, therefore, potentially influence the hydrological cycle and climate as nuclei for water droplets and ice crystals in clouds, fog, and precipitation (Frohlich-Nowoisky and Poschl, 2013; Pouleur et al., 1992).

2.2. Oligotrophic conditions

There is increasing evidence that in nature, fungi commonly exist in conditions of nutrient depletion. There is a wide range of

nutritional heterogeneity within soil, e.g. from the nutrient-rich rhizosphere to habitats containing low amounts of available organic material (Wainwright, 1993). Mineral soil in particular can be a poor source of available carbohydrate (Wainwright, 1993; Wainwright et al., 1991). Despite this, many fungi can maintain growth in soil and other nutrient-limited habitats (Wainwright, 1993; Wainwright et al., 1991). It has been suggested that these organisms possess characteristics that enable them to utilize low nutrient supplies efficiently including an increased capacity to take up nutrients by possessing a high surface area resulting from sparse but extensive mycelium, high affinity nutrient uptake sites, and translocation of nutrients from a nutrient-rich base (Boswell et al., 2002; Jacobs et al., 2004; Ritz, 1995; Wainwright, 1993; Wainwright et al., 1993). Germ tubes and hyphae may be reduced in diameter and length when compared to similar structures in carbon-rich conditions. Nutrients may also be recycled through cryptic growth, where the tips of the hyphae grow at the expense of preformed fungal material (Schnurer and Paustian, 1986). It is also possible that carbon dioxide and other gases, and volatiles including hydrocarbons, alcohols, aldehydes, ketones and phenols may be scavenged from the environment and act as a source of fungal nutrition (Fries, 1973; Tribe and Mabadeje, 1972; Wainwright, 1993).

It is predictable therefore, that the responses of fungi towards other stresses, e.g. toxic metals and xenobiotics, will be affected by the nutritional status of the habitat. In a low-nutrient environment, there may be a limitation to expression of both direct and indirect mechanisms of tolerance/resistance, as well as effects on metabolism, growth and branching. Toxic metals can have a significant impact on the overall length of the fungal mycelium and branching patterns, with responses being affected by nutrient availability (Ramsay et al., 1999). *Trichoderma viride* and *Rhizopus arrhizus* appeared to exhibit ‘foraging’ modes of growth on low-substrate media with sparse colonies formed (Ritz, 1995), and Cu and Cd were capable of disrupting this explorative growth under laboratory conditions resulting in alterations to the distribution of the fungal biomass (Ramsay et al., 1999). Conidia of the insect-pathogenic fungus *Metarhizium robertsii* produced under nutritive stress (Czapek medium without sucrose) accumulated two-folds more trehalose and mannitol and became two-folds more virulent and tolerant to UV-B radiation and heat than conidia produced on potato dextrose agar supplemented with yeast extract (Oliveira et al., 2018; Rangel, 2011; Rangel et al., 2006a, 2008a, 2008b, 2012, 2015c). If manifest in natural environments, such responses may influence success in locating nutrients as well as survival capability.

2.3. Ionizing radiation

An extreme man-made habitat with elevated levels of ionizing radiation was created by the atomic bombardments of Hiroshima and Nagasaki in 1945, nuclear power plants accidents such as Three Mile Island in the United States in 1979 (Hultman and Koomey, 2013), Chernobyl in Ukraine in 1986 (Zhdanova et al., 2000), and Fukushima Daiichi in Japan in 2011 (Koarashi et al., 2014), as well as other nuclear accidents such as the Goiania accident in Brazil in 1987 (Godoy et al., 1991). Several studies of fungal resistance to ionizing radiation have been performed (Dadachova and Casadevall, 2008; Dighton et al., 2008; Mitchel and Morrison, 1982; Petin and Komarov, 1997; Zhdanova et al., 2000). *Cryomyces antarcticus*, which occurs endolithically in the McMurdo Dry Valleys of Antarctica, in the fully hydrated state can survive doses of up to 5000 Gray (Gy), and much higher doses in the dried state (Selbmann et al., 2017) and are among the most radioresistant organisms on the planet, along with the bacterium *Deinococcus radiodurans* (Daly et al., 2004; Ito et al., 1983), and an animal

tardigrade (Horikawa et al., 2006). For comparison, an acute dose of 5–10 Gy would kill a human (Hall and Giaccia, 2011) and 200–800 Gy would kill *Escherichia coli* (Harris et al., 2009). When exposed to high doses of gamma radiation of up to 8000 Gy, which are lethal for the majority of non-melanized fungi, melanized forms are able to survive, with melanin playing a role of a radioprotector (Dadachova et al., 2008). In addition, melanin protects the fungi *Cryptococcus neoformans* and *C. antarcticus* from highly energetic and damaging particulate radiation such as deuterons (Pacelli et al., 2017a, 2017b). Moreover, when exposed to non-lethal doses several times above the background radiation - melanized fungi grow better than their non-melanized counterparts (Dadachova et al., 2007; Robertson et al., 2012) implying that in such situations melanin plays a role as an energy transducer, allowing fungal cells to utilize the converted energy of ionizing radiation in their metabolic processes. The computer modelling of this dual relationship between melanized fungi and ionizing radiation revealed that these phenomena occur within a wide range of radiation doses, energies, and dose rates (Shuryak et al., 2014). A possible mechanism of interaction between melanin in fungi and ionizing radiation involves Compton scattering of incident photons by the conjugated aromatic rings of the melanin structure with the simultaneous trapping of resulting Compton electrons by the melanin stable free radical (Schweitzer et al., 2009). Electrochemical and electron spin resonance (ESR) investigations have demonstrated that melanin is oxidized during this process but is capable of self-repair by attracting electrons from the environment (Khajo et al., 2011; Turick et al., 2011). Such unique properties of fungal melanin may have potential applications in radioprotection of patients undergoing radiation therapy (Revskaia et al., 2012), in environmental remediation, and in creating genetically modified plants capable of using melanin and ionizing radiation in a process similar to photosynthesis (Dadachova and Casadevall, 2008).

2.4. Solar ultraviolet radiation

Solar radiation is essential to life on Earth, but its UV component may also harm living organisms. Ultraviolet radiation was first separated into three wavelength categories at the Copenhagen Meeting of the Second International Congress on Light in 1932, dividing the UV spectrum into UV-C (shorter than 280 nm), UV-B (280–315 nm), and UV-A (315–400 nm) wavelengths (Coblentz, 1932). Presently, however, many reports use 320 nm as the division between the UV-A and UV-B wavebands (Braga et al., 2015). UV-C radiation does not penetrate to the ground due to strong absorption by atmospheric gases including oxygen (Paul, 2000). The Earth's surface is also largely protected from the most damaging short wavelength UV-B radiation due to absorption by stratospheric ozone. UV-A radiation passes through the atmosphere with little attenuation and is thus the largest component of ground-level solar UV radiation (Williamson et al., 2014). The UV-B radiation from the sun may increase as a result of ozone depletion in the Earth's stratosphere, which is caused by man-made pollution (McKenzie et al., 2007). This increased solar UV-B radiation will have immense consequences for agriculture. Although plants are more tolerant to UV-B radiation than other organisms, it is known that UV-B radiation causes physiological changes (e.g. reduced net photosynthesis, changes in chemical composition, changes in pigment levels, premature ripening, and senescence) as well as morphological changes (e.g. increased branching, leaf thickness, and leaf size, as well as stunted growth) (Caldwell et al., 2007; Flint et al., 2004). In addition, increased solar UV-B radiation strongly affects microorganisms that are important for agriculture such as the plant pathogen antagonists *Trichoderma harzianum* and *Trichoderma viridae* (Braga et al., 2002; Moody et al., 1999; Paul et al.,

2005), fungi and bacteria used to control insect agricultural pests (Braga et al., 2001a, b; Braga et al., 2001c; Dias et al., 2018; Myasnik et al., 2001; Rangel et al., 2006b), fungi to control insect vectors of disease (Luz et al., 2004; Santos et al., 2011), and decomposer microorganisms (Giordano et al., 2003; Moody et al., 1999; Pancotto et al., 2003). UV-B radiation can also change the species composition and biodiversity of bacterial and fungal communities growing on plants. For pathogens, elevated UV-B can either increase or decrease the severity of disease development in plants depending on the fungal-plant-pathogenic species (Caldwell et al., 2003; Paul et al., 1997).

2.5. High temperatures

Another source of stress is the heat produced by solar irradiation or convection. Depending on the soil type, solar heat may cause the temperature of the bare-soil within 5 cm of the surface to reach temperatures of up to 65 °C - this phenomenon has been reported during the rainy season in the Niger Republic, West Africa (Arthurs et al., 2001). Bare soil surfaces subjected to full sunlight reached 60 °C in irrigated corn fields in Logan, Utah, USA in mid-July at 5:00 pm (Rangel et al., 2005b). Thus, resistance to heat represents an important adaptive trait for many microbial communities. Usually germlings and mycelia are much more susceptible to heat (Rangel et al., 2010) than their counterpart conidia (Rangel et al., 2005b; Souza et al., 2014). Heat stress has great influence on soil microbes; for example, isolates of insect-pathogenic fungi *Metarhizium* spp. collected from above latitude 40 North or South are less heat tolerant than isolates collected from close to the equator (Rangel et al., 2005b). In addition, a population genetics analysis of the insect-pathogenic fungus *Metarhizium anisopliae* from forested and agricultural habitats in Ontario, Canada found that the group from forested areas has an ability for cold-active growth at 8 C and is less tolerant to heat, while the group from the agricultural area showed an ability for growth at high temperatures at 37 C and they are less cold-active (Bidochka et al., 2001). Man-made global warming is predicted to increase the annual mean surface temperature of earth even more; this will, no doubt, bring extreme changes in the Earth's surface microbial populations. Allison et al. (2010) pointed out a different effect of heat: burning of a boreal fire can deplete carbon from soil. This, in turn, increased the resistance of a fungal community to soil warming. Similarly, fungal communities from sand mining degraded soil, which is carbon depleted and intensely heated, are more heat and UV-B tolerant than the fungal communities after the ecological restoration of this same area with native trees (Ferreira et al., 2018).

2.6. Cold temperatures

Fungi can be isolated from extremely cold environments, including permafrost, deep seas, snow and polar environments (Gunde-Cimerman et al., 2003). Physiological mechanisms conferring cold tolerance in fungi are complex and include accumulation of chaotropic metabolites (e.g. fructose and glycerol), increases in intracellular trehalose and other polyols, and unsaturated membrane lipids as well as secretion of antifreeze proteins and possession of enzymes active at low temperatures (Chin et al., 2010; Robinson, 2001). Furthermore, fungi with dark septate hyphae may dominate the microbial community in Antarctic, Arctic and alpine soils. Melanins may protect these organisms from extreme temperatures and drought, and play a significant role for persistence of hyphae from year to year in such environments (Robinson, 2001). Cold-adapted fungi are a potential source for novel bioactive secondary metabolites and enzymes (Rateb and Ebel, 2011; Wang et al., 2015).

2.7. Acidity and alkalinity

One of the most influential factors that can affect microbial communities in soil is pH since it strongly influences nutrient availability and metal mobility, and community composition of fungi and bacteria. In general, acidic pH values favour fungal growth which results in an increase in the dominance and relative importance of fungi compared to bacteria under acidic soil conditions such as in coniferous soil. Apart from this, many fungi can grow over a wide pH range from extreme acidity to alkaline conditions (Magan, 2007). Many alkalitolerant and alkaliphilic species are known (pH 8–11), isolated from alkaline environments such as soda soils, calcareous deposits, and ammonia and urea-enriched soils (Grum-Grzhimaylo et al., 2016; Li et al., 2015). Alkaliphily may be associated with morphological responses such as darkly pigmented mycelium, formation of microsclerotia or other enclosed fruit bodies, extensive production of extracellular polymeric materials (EPS), and hyphal aggregation in chords (Grum-Grzhimaylo et al., 2016). Furthermore, fungi, including lichens, are important biodeteriogens in the built environment and are well known to have significant effects even on alkaline substrates such as concrete, cement, mortars and plaster (Gadd, 2017a). It is now known that many fungi inhabit extremely acidic environments, including yeasts and filamentous forms (Aguilera et al., 2006; Baker et al., 2004; Gross and Robbins, 2000). Some filamentous species isolated from acidic environments are some of the most acidophilic microorganisms that have been documented, e.g. *Acontium cylatium*, *Trichosporon cerebriae* and a *Cephalosporium* sp. have all been reported to grow at around pH 0 (Aguilera et al., 2006; Magan, 1997; Schleper et al., 1995). The physiological basis for alkaliphily or acidophily in fungi has received scant attention, although there is evidence for vacuolar involvement in H⁺ homeostasis under extreme acidity (Magan, 2007). A *Penicillium ochro-chloron* strain capable of growth in high concentrations of copper sulfate at very low pH synthesised high amounts of glycerol allowing growth in such conditions, with copper uptake being greatly repressed under such low acidity (Gadd et al., 1984; Gadd and White, 1985).

2.8. Osmotic stress

In several environments fungi will encounter hyperosmolarity and low water potentials caused by the presence of high concentrations of salts and sugars. Fungi are found in several natural locations such as alkaline soda Wadi El-Natron Lakes in Egypt (Moubasher et al., 2013), or in the alkaline and hypersaline Mono Lake in California, USA (Steiman et al., 2004) and on the Dead Sea shore located in the Syrian-African rift valley, on the border between Israel and Jordan (Kis-Papo et al., 2003), as well as dry surfaces such as wood and pages of books (Williams and Hallsworth, 2009). The ability to survive osmotic stress requires several adaptations in fungi involving osmoregulation (Hohmann, 2002), ion transport and homeostasis (Serrano et al., 1999), sodium extrusion (Almagro et al., 2001), and melanin synthesis (Kogej et al., 2007). Under these conditions, fungi adjust their internal solute potentials by accumulation of solutes such as glycerol, erythritol, mannitol, and trehalose, which reduces internal water potential and limits osmotic losses (Dijksterhuis and de Vries, 2006; Hallsworth and Magan, 1994; Rangel, 2011; Rangel et al., 2008b, 2015c). In addition, they modify the plasma membrane (Turk et al., 2004), increase cell wall thickness (Kralj Kuncic et al., 2010) and in some cases, as observed in halotolerant fungi such as *Cladosporium cladosporioides*, they accumulate mycosporines (Oren and Gunde-Cimerman, 2007). Osmotic stress also causes an increase in fatty acid unsaturation in the membranes (Turk et al., 2004), as well as modifications in the morphology of fungal cells (Kogej et al., 2006; Kralj Kuncic

et al., 2010; Rangel et al., 2008b) and colonies (Kogej et al., 2006; Kralj Kuncic et al., 2010).

Some fungal species are known to be halotolerant, osmotolerant, or xerotolerant. Such fungi includes the melanized *Cladosporium* species, that are found in hypersaline waters around the world (Butinar et al., 2005a; Cantrell et al., 2011; Gunde-Cimerman et al., 2000). *Cladosporium* has also been found in other extreme habitats, such as stratosphere (Della Corte et al., 2014), or rocks of the Atacama Desert (Gonçalves et al., 2016), which are known to have a very low water activity. Another member of indigenous fungal communities in hypersaline waters of salterns, includes the genus *Eurotium* (Butinar et al., 2005b; Stevenson et al., 2015b), that can grow at 0.70 water activity (a_w) (Magan, 2001; Stevenson et al., 2015b) and even lower (Stevenson et al., 2015a). Another extreme halophile is the fungus *Aspergillus penicillioides*, which is able to germinate at 0.585 a_w (approximately 58.5 % relative humidity), which is now considered the limit for life (Stevenson et al., 2017).

2.9. Toxic metals

Anthropogenic activities, including fossil fuel combustion, mineral mining and processing, release of industrial effluents and sludges, biocides and preservatives, redistribute a variety of toxic metal species into aquatic and terrestrial ecosystems which can have significant effects on the biota (Gadd, 2016). In addition, metals are involved in almost all geomicrobial processes, and their transformations and alterations in mobility are important in bioweathering, mineral formation and dissolution, and soil formation (Gadd, 2010). Metals, metalloids, metal radionuclides, organometals and organometalloids, and their compounds, interact with fungi in various ways depending on chemical speciation, organism and environment, with the fungi also able to influence metal speciation and mobility (Gadd, 2017a, 2018; Gadd et al., 2012). Many metals are essential for life, e.g. Na, K, Cu, Zn, Co, Ca, Mg, Mn, and Fe, but all can be potentially toxic when present above certain threshold concentrations. Other metals, e.g. Cs, Al, Cd, Hg and Pb, have no known metabolic function in fungi but can still be accumulated. Metal toxicity is affected by physico-chemical conditions and the chemical behaviour of the particular metal species (Fomina et al., 2005; Gadd, 1993; Howlett and Avery, 1997). However, fungi are ubiquitous in metal-polluted locations and a variety of direct and indirect mechanisms contribute to their survival. Such mechanisms include reduction of metal uptake and/or increased efflux, metal immobilization by, e.g. biosorption to cell walls and exopolymers, mineral bioprecipitation, intracellular sequestration, and localization in vacuoles (Gadd, 1993, 2007, 2010). Such mechanisms by which fungi (and other microorganisms) change metal speciation and mobility not only influences survival but are also important components of biogeochemical cycles for metals, and other elements that may be associated with organic and inorganic substrates including carbon, nitrogen, sulfur and phosphorus (Gadd, 2004, 2006, 2007, 2008). In some cases, wall structure and composition is affected by the presence of toxic metals and this may in turn influence colony development and morphology (Ramsay et al., 1999). A variety of toxic metals can induce or accelerate melanin production in fungi, leading to blackening of colonies and chlamydospore development (Gadd and Griffiths, 1980). Melanized forms have high capacities for metal biosorption, with the majority of metal remaining within the wall structure (Gadd et al., 1984; Gadd and Mowll, 1985). Synnema are defined as aerial, multihyphal structures where the apices of the component hyphae advance together and ultimately form spores (Watkinson, 1979). They are therefore concerned with the spread and survival of a given species and their formation can be triggered by a variety of external factors and stresses, e.g. light–dark

transitions, low temperature, alcohols, detergents, carbon dioxide, amino acids and certain metal compounds (Newby and Gadd, 1987; Watkinson, 1979).

2.10. Xenobiotics

Fungi, as well as other microorganisms, encounter a broad spectrum of antimicrobial compounds in their environments and often possess metabolic strategies to detoxify such xenobiotics. These can include anthropogenic pollutants such as pesticides, polycyclic aromatic hydrocarbons (PAH), and other persistent organic pollutants (POP), as well as many antifungal substances produced by a broad spectrum of organisms (Jenssen et al., 2006; Tincu and Taylor, 2004). The latter compounds include peptides, fatty acids, proteins, alkaloids, quinones, and statins. Survival necessitates expression of effective antioxidant mechanisms and the most common processes used by fungi in resistance to antifungal agents are destruction of the agent, changes in the target enzyme or pathway by mutation, and active efflux to maintain low intracellular concentrations (Barabote et al., 2011; Cowen and Steinbach, 2008; Ghannoum and Rice, 1999). Some fungi have remarkable degradative properties and lignin-degrading white rot fungi, such as *Phanerochaete chrysosporium*, can degrade several xenobiotics including aromatic hydrocarbons, chlorinated organics, polychlorinated biphenyls, nitrogen-containing aromatics and many other pesticides, dyes and other xenobiotic (Gadd, 2004; Magan et al., 2010). Such behaviour is of relevance to bioremediation of such substances although co-metabolism of a more easily utilisable carbon source may be additionally required, as well as beneficial interactions with bacterial communities (Gadd, 2004). Many xenobiotic substances induce chaotropy-mediated cellular stresses in fungi and other microbes, and induce a chaotropy-specific stress response including production of protein-stabilization proteins and changes in membrane composition (Cray et al., 2015; Hallsworth, Heim et al., 2003a; Hallworth, et al., 2003b).

2.11. Rock and mineral-based substrates

Due to their filamentous growth habit and ability to produce and exude organic acids, protons and other metabolites, fungi are ideal biological weathering agents of rocks, minerals and building materials. Fungi are ubiquitous components of the microbiota of all rocks and building stone and they have been reported from a wide range of rock types including limestone, marble, granite, sandstone, basalt, gneiss, dolerite and quartz, even from the most harsh environments, e.g. hot and cold deserts (Gorbushina, 2007; Staley et al., 1982; Sterflinger, 2000; Verrecchia, 2000). Furthermore, fungi are considered to be the most important colonizers of stone, mortar and plaster (Scheerer et al., 2009; Sterflinger, 2000, 2010). Sub-aerial rock surfaces may be thought an inhospitable habitat for fungal growth due to moisture deficit and nutrient limitation although many species are able to deal with varying extremes in such factors as light, nutrient availability, salinity, pH, and water potential, over considerable periods of time. The presence of organic and inorganic residues on mineral surfaces or within cracks and fissures within the mineral substrate can encourage proliferation of fungi and other microbes as well as the waste products of algae and bacteria, dead cells, decaying plant material, dust particles, aerosols and animal faeces (Sterflinger, 2000). The ability of many fungi to grow oligotrophically by scavenging nutrients from the air and rainwater also helps them survive on stone and rock surfaces (Gorbushina, 2007; Wainwright, 1993). Stone-inhabiting microorganisms may grow on the surface (epilithic), in crevices and fissures (chasmolithic), or may penetrate some millimetres or

even centimetres into the rock pore system (endolithic), thereby gaining protection from environmental extremes and fluctuations (Gadd, 2017b; Gorbushina, 2007; Hoppert et al., 2004). Some fungal groups exhibit microcolonial or yeast-like growth forms that are effective in providing protection from heat and desiccation (Gorbushina, 2007). These may prevail under harsh conditions, and appear as black spots due to possession of UV-protective melanins (Gorbushina, 2007; Gorbushina and Broughton, 2009). This growth habit confers a high degree of resistance to environmental stresses and these organisms are considered the most persistent inhabitants of exposed rock surfaces. One of the most successful means for fungi to survive in the extreme sub-aerial environment is underpinned by their symbiotic associations with algae and cyanobacteria as lichens where the phototrophs provide a source of carbon and protection from light and irradiation (Sterflinger, 2000). Lichens enable colonization of a wide range of environments including those at climatic extremes such as the Arctic and Antarctic, exposed rock surfaces and dry deserts (Gadd, 2017b).

2.12. Deep subsurface

In the deep subsurface, the research emphasis is mostly on prokaryotes, but the presence of fungi is now well known (Ivarsson, 2012; Ivarsson et al., 2016; Nagano and Nagahama, 2012; Orsi et al., 2013). Fungi occur in abundance and high diversity in such varied environments as deep-sea sediments (Nagano et al., 2010), hydrothermal vents (Connell et al., 2009; Le Calvez et al., 2009), and methane cold-seeps (Nagahama et al., 2011; Nagano et al., 2010). They are now also known as abundant inhabitants of the igneous oceanic crust which has consequently been described as the largest fungal habitat on Earth (Ivarsson et al., 2016). Fungi seem to play an important ecological role in the igneous oceanic crust as they exist in symbiosis with chemolithotrophic prokaryotes, decompose organic matter, dissolve and form minerals, and therefore are involved in the cycling of elements (Bengtson et al., 2014; Ivarsson et al., 2015, 2016). Fossilized microorganisms have been observed in drilled cores and dredged samples from the ocean floor with a majority of these findings representing fungi (Bengtson et al., 2014; Schumann et al., 2004). These fungi existed in a close symbiotic-like relationship with two types of prokaryotes, which appeared to use the structural framework of the mycelium for their growth (Bengtson et al., 2014). It therefore seems clear that geomycological processes are significant in a wide range of biosphere habitats, including those traditionally thought to be inimical to fungal growth and development (Gadd, 2006).

3. Fungal stress in agriculture and forestry

Many important pathogens of crop plants in forestry and agriculture are fungi but fungi are also increasingly used as commercial biological control agents to control plant diseases (Butt et al., 2001). In coniferous forests *Heterobasidion* fungi cause economically devastating root rot diseases causing financial losses of 790 M € each year in Europe alone. However, application of the fungus *Phlebiopsis gigantea* to root stumps during tree felling can result in 95–100 % reduction of the disease with little apparent impact on other soil fungi (Menkis et al., 2012). Biocontrol has typically been approached from the point of view of how antagonists attack pathogens and there are far fewer studies of how fungal pathogens respond to the biological stress induced by antagonists (Duffy et al., 2003; Gkarmiri et al., 2015). These self-defense responses are diverse, including detoxification, repression of synthetic biocontrol genes, active efflux of antibiotics, and antibiotic resistance. Under some conditions, biological control agents can even, unexpectedly, promote growth of the fungal pathogen (Cray et al., 2016). A better

understanding of the mechanisms involved will aid the development of more efficient antagonists. Many fungi have been developed into commercial biological control agents and are being mass produced to be used in agriculture to promote plant growth (Vega et al., 2009), promote plant defense responses (Vega et al., 2009), and to control plant diseases (Costa et al., 2012, 2013; Druzhinina et al., 2011; Smith et al., 1998), plant parasitic nematodes (Siddiqui and Mahmood, 1996), terrestrial weeds (Moraes et al., 2014), aquatic weeds (Cothier and Gilbert, 1994), and insects (Alston et al., 2005; Keyser et al., 2017; Li et al., 2010). Different abiotic environmental factors cause stress and consequently harm these important fungi in agricultural systems, and fungi that are applied to the aerial parts of plants, such as insect pathogens, are especially susceptible to solar UV radiation (Braga et al., 2001a, b; Braga et al., 2002; Fargues et al., 1996; Rangel et al., 2005a) and heat (Rangel et al., 2005b, 2010; Santos et al., 2011; Souza et al., 2014) that cause reductions in their activity. Fungi that control weeds (mycoherbivores) are also affected by UV-B radiation (Cliquet et al., 2011; Texier et al., 2009).

Symbiotic mycorrhizal fungi play important roles in stress tolerance in both agricultural and forest ecosystems, improving nutrient uptake and drought tolerance, restricting base cation leaching and mitigating the toxic effects of elevated heavy metals and aluminum (Finlay et al., 2009; Finlay, 2008). Different types of mycorrhizal symbiosis have very different effects in different systems and carbon allocated by the plants to their fungal symbionts may be used for fungal production of siderophores or enzymes used to mobilize organic polymers of nitrogen or phosphorus, glycoproteins that stabilize soil aggregates, or priming of bacteria involved in solubilizing phosphorus or other types of plant growth promotion (Finlay, 2008). Carbon flow in the rhizosphere or “mycorrhizosphere” may have important consequences for mitigation of effects of plant diseases or interactions with decomposers and thus be of significance in the sustainability of low-input cropping systems (Johansson et al., 2004; Jones et al., 2009). Fungi may also influence global patterns of carbon sequestration. Clemmensen et al. (2013) demonstrated that at least half of the accumulated carbon in humus layers of boreal forested islands originated from root-derived inputs rather than from above-ground plant litter inputs. More recent results of Clemmensen et al. (2015) suggest that at earlier successional stages, the high abundance of cord-forming ectomycorrhizal fungi implies efficient recycling of carbon and nitrogen, whereas in older ecosystems, stress-adapted, root-associated ascomycetes generally seem to promote biochemical stabilization of these compounds in organic matter derived from mycelium. Recent studies of arbuscular mycorrhiza in agricultural systems suggest that AM fungi improve drought tolerance and tolerance of salinity of their plant hosts through improved nutrient uptake, accumulation of organic solutes and reduced oxidative stress due to enhanced activity of calmodulin, superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase (Abdel Latef and Chaoping, 2014; Chandrasekaran et al., 2014; Huang et al., 2014).

Assigning trophic strategies to filamentous fungi is complicated by the fact that their mycelia may simultaneously interact with different substrates in different ways. An example of this is the entomopathogenic fungus *M. robertsii* that can transfer insect-derived N to plants, promoting their growth (Behie et al., 2012) while this process is driven by reciprocal allocation of C from the plant roots to the fungal mycelium (Behie et al., 2017).

A recent study by Liao et al. (2014) using *Zea mays* colonization of plant roots by different wild type and mutant *Metarhizium* strains suggested that the fungi were plant growth promoters irrespective of their role as insect pathogens and that colonization of roots was a pre-requisite for most if not all of their beneficial

effects. Other groups of (non-mycorrhizal) fungi that are well-known for mediating stress reactions in plants include species of the genus *Trichoderma*, which show a wide range of lifestyles but are able to antagonize or parasitize plant-pathogenic fungi and to stimulate plant growth and defense responses (Druzhinina et al., 2011), and species such as *Piriformospora indica*, which can promote the growth of a spectrum of plants by inducing disease resistance and tolerance of salt stress through a systemic elevation of the antioxidative capacity mediated by the glutathione-ascorbate cycle (Waller et al., 2005). There is growing interest in plant biostimulants to enhance plant growth (Calvo et al., 2014) and clear potential for exploiting fungal stress responses to access novel molecules that can be used in agriculture. Fungal endophytes have also been discussed as an important reservoir of novel antibacterial substances with therapeutic potential (Deshmukh et al., 2014). Induction of tolerance to heat stress in naturally growing plants colonized by fungal endophytes (Redman et al., 2002) has also been shown to occur in wheat, increasing grain yield, seed germination, and drought tolerance (Hubbard et al., 2012, 2014). Other more recent studies of symbiotically conferred stress tolerance (Rodriguez et al., 2008) suggest that it arises as a result of habitat-adapted symbiosis and that it may have considerable potential in mitigating impacts of climate change in different cropping systems, as well as expanding agricultural production onto marginal lands (Redman et al., 2011).

In conclusion, fungi perform important functions in a variety of natural processes, including effects on soil fertility and plant productivity, decomposition of organic matter, cycling of minerals, plant health, and food production and consumption. Successful exploitation of fungi requires better understanding of the mechanisms that fungi use to cope with stress, as well as of the ways in which they mediate stress tolerance in other organisms.

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