Fungal Biology 122 (2018) 602–612

Contents lists available at ScienceDirect

Fungal Biology

journal homepage: www.elsevier.com/locate/funbio

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

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A R T I C L E I N F O

Article history:
Received 30 November 2017
Received in revised form
5 February 2018
Accepted 9 February 2018
Available online 16 February 2018

Corresponding Editor: Geoffrey Michael Gadd

Keywords:
Aeromicrobiology
Biotic stress
Growth promotion
Ionizing radiation
Mediation of plant stress
UV radiation

A B S T R A C T

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.

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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https://doi.org/10.1016/j.funbio.2018.02.002
1878-6146/

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 Leewenhoeck, 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), nd 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