10.2 Ecological Stress: Melanization as a Response in Fungi to Radiation

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Introduction

Fungi are known as organisms highly adapted to their environment. Among various extremes they need to cope with when colonizing natural and man-made substrates is a high level of radiation of different kinds – solar (UV) or ionizing. In the last decades, a significant reduction in the stratospheric ozone layer has been registered, with ozone loss between 1979 and 1991 averaged around 4 ± 6% per decade at northern temperate latitudes (Hollandsworth et al. 1995). As a result, the amount of more harmful UV-B radiation (280–315 nm) reaching the Earth's surface has increased (e.g., Kerr and McElroy 1993). In parallel, contamination of the environment by radionuclides, a source for the ionizing radiation, is also enhanced. All these man-induced environmental changes increase the necessity to withstand high radiation levels, and the protective role of dark pigmentation mainly of melanin nature in surviving and exploiting highly radiated environments is confirmed to be crucial.

What is Fungal Melanin?

Melanin (Greek *melas*) is a pigment of high molecular weight composed of various types of phenolic or indolic monomers usually associated with protein, and often with carbohydrates. Detailed description of fungal melanin types, their chemical structure, and pathway is given in the comprehensive reviews of Bell and Wheller (1986) and Butler and Day (1998). Numerous studies have shown that fungal melanin is always located in the cell wall, either entangled within the structure of the wall, or as its outermost layer, and may be granular or fibrillar (Butler and Day 1998 and references therein).

UV-Protective Functions of Fungal Melanin

Melanin pigments are found in all kingdoms of living organisms thus revealing their ancient origin. Melanized fungal spores in large quantities have been discovered in the deposits of early Cretaceous period when many animal and plant species died out (Dadachova and Casadevall 2008). In that period, Earth crossed the "magnetic zero" causing the loss of its protective "screen" against cosmic radiation (Hulot and Gallet 2003). And so far, the science has accumulated a large body of knowledge, both from nature and laboratory experiments, evidencing on the radioprotective role of melanin pigments in interactions of fungi with their environment.

Air

The atmosphere usually contains fungal spores in high concentrations reaching 10^4 spores per m^3, which is much higher than concentrations of bacterial cells – of the order of 10^3 cells per m^3 in the air of a large town and 10^2 cells per m^3 in the countryside (Yanagita 1990). Dominance or frequent occurrence of dematiaceous airborne fungal species has been well documented all over the world – for example, in Spain (dominance of the genera *Cladosporium*, *Ustilago*, *Pleospora* – Herrero et al. 2006), in Israel and Turkey (*Cladosporium*, *Alternaria* – Waisel et al. 1997; Sen and Asan 2001, respectively), in Lithuania (*Cladosporium*, *Alternaria*, *Aspergillus niger* – Lugauskas et al. 2003), in Brazil (*Cladosporium*, *Leptosphaeria*, *Alternaria* – Zoppas et al.

2006), and in Africa (*Cladosporium*, *Alternaria*, *Arthrinium*, *A. niger* – Prospero et al. 2005). Even some frequently recorded in the air spores of light-colored fungi from the genera *Penicillium* and *Aspergillus* are known to contain greenish pigments of a melanin nature (e.g., Coelho et al. 1997; Cuadros et al. 1999; Youngchim et al. 2004). Field study of the responses of airborne fungi to UV-B radiation in the coastal area of Lithuania has shown that predominantly dark-colored sporulated and non-sporulated species were documented after exposure to the radiation (Ulevicius et al. 2004). Protective pigmentation of cell walls with melanin and melanin-like pigments is considered to make airborne fungal propagules less vulnerable to the UV radiation damage compared to bacterial cells.

Leaf Surface

The plant leaf surface, or phyllosphere (phylloplane), supports the growth of diverse fungal biota. Just simply counting the percentage of melanin-containing species in such phyllosphere mycobiota from the British Isles containing near 4,300 species described in the classic book of Ellis and Ellis (1997) shows overwhelming dominance of melanized species – more than 95% of species composition. Most of them have double (dark color of fruit bodies and ascospores or conidia and mycelia) or even triple (dark color of fruit bodies, spores, and mycelia) defense against direct exposure to UV radiation. Microfungal communities from plant leaves collected in the Mediterranean area in Portugal (Pereira et al. 2002) provides another characteristic example from the numerous on this topic. Here, melanin-containing *Aureobasidium pullulans*, *Cladosporium cladosporioides*, *C. spherospermum*, and *Alternaria alternata* comprised more than 80% of total fungal isolates. Laboratory experiments on survival rates of some dark-colored phylloplane-inhabiting fungi from the genera *Alternaria*, *Ulocladium*, and *Epicoccum* under short wavelength UV radiation (250–270 nm) demonstrated their much higher resistance to the treatment in comparison with lighter pigmented *Botrytis cinerea*, which had also conidia with thinner cell walls (English and Gerhardt 1946; Boyd-Wilson et al. 1998). Such UV-resistant leaf surface fungi, mainly from the genera *Alternaria*, *Cladosporium*, and *Phoma* were found to be considerable contributors to the air spora (Hameed and Awad 2005; Levetin and Dorsey 2006).

Rock Surface

Bare rock surfaces in hot and cold deserts as well as in high mountains represent terrestrial environments most hostile and extreme for any kind of life (e.g., Shilo 1978). But in spite of the hostility, rock surfaces and more specifically, rock varnish (Perry et al. 2003) are persistently inhabited by a very specialized group of free-living microscopic fungi (e.g., Staley et al. 1982; Sterflinger and Krumbien 1995; Gorbushina 2003). These rock-dwelling fungi develop very small colonies both in situ and in vitro and are called microcolonial fungi (MCF). MCF not only survive but grow under extremely stressful environmental conditions including high UV radiation and, again, black pigments highly concentrated in their cell walls serve as UV-protective substances (e.g., Urzi et al. 1995). Melanin is located in the cell walls of black fungi and yeasts as an external electron-dense granular layer as well as in the matrix between the cells forming an extracellular intracolonial structure (Gorbushina 2003). Along with melanin pigments, other groups of UV-absorbing compounds of low molecular weight, mycosporines, have been found in MCF (Gorbushina et al. 2003). Mycosporines have a unique absorption spectrum of

310–320 nm (Bandaranayake 1998) and can serve as specialized structures enhancing the survival potential and longevity of rock-inhabiting microfungi (Gorbushina et al. 2003).

Specific fungal life has been discovered in the lichen-dominated cryptoendolithic communities colonizing rocks in the Antarctic ice-free desert. Two new genera and four new species of black MCF, probably endemic, have been described using morphological and molecular analyses (Selbmann et al. 2005). Strains of *Cryomyces minteri* and *C. antarcticus* tested for their UV resistance were highly resistant to UV-B irradiation showing long-time survival and no morphological modifications at both colony and cellular levels after the treatment (Onofri et al. 2007). The species were found to express melanized thick walls as a stable characteristic, allowing them to tolerate dryness and the UV irradiation that reaches them through the translucent crystals of orthoquarzite in sandstone (Selbmann et al. 2005). The tested strains of *Cryomyces* have been considered as good candidates to be exposed to the space and simulated Mars conditions, including space vacuum, solar UV, and cosmic radiation (Onofri et al. 2007).

Not only specific microcolonial fungi, but also common black fungi from the genera *Phoma* and *Alternaria* were found to cause physical and chemical damage (blackening and brown patinas) of sandstones, limestones, and marbles collected from monuments and rock outcrops throughout Europe and Africa (Diakumaku et al. 1995). Most of the strains examined produced pigments of a melanin nature responsible for staining of the rocks under extreme environmental conditions including high persistent irradiation.

Soil and Litter

UV radiation is known to penetrate only up to about 100 microns into soil depth (Johnson 2003) but in the uppermost layers of sun-exposed soils, this environmental factor plays an important role in the organization of microfungal communities. Non-surprisingly, dominance of dark-colored microfungi is characteristic for almost all mycologically studied desert soils (e.g., Ranzoni 1968; Christensen 1981; Halwagy et al. 1982; Skujins 1984; Abdullah et al. 1986; Hashem 1991; Ciccarone and Rambelli 1998; Mulder and El-Hendawy 1999, Zak 2005). In the Negev desert, Israel, melanin-containing microfungi comprised 55% of general species composition and strongly prevailed in relative abundance (58–77% in different localities). Importantly, melanized fungi with large thick-walled multicelled conidia increased their abundance southward in open localities of northern and central Negev (Grishkan et al. 2006) and overwhelmingly dominated all microfungal communities in southern Negev (Grishkan et al. 2007). These fungi were mainly represented by *Ulocladium atrum*, *U. botrytis*, *Alternaria alternata*, and *A. chlamydospora*. The first three species are cosmopolitan, the latter one a desert fungus, which also produces large multicelled chlamydospores (Ellis 1971, 1976). The multicellular spore morphology, together with melanin pigmentation, should be considered as an important adaptive feature of desert soil mycobiota. Spores of such morphology can successfully survive under UV radiation, extreme temperatures, and drought. In nature, species with dark, multicelled conidia isolated from the Negev uppermost soil layer are also phylloplane inhabiting (Ellis 1971, 1976; Ellis and Ellis 1997). Under laboratory conditions, Durrell and Shields (1960) showed that the survival time of thick-walled multicellular conidia of *Stemphylium ilicis* under the same irradiation was 30-fold longer than for thin-walled one-celled conidia of *A. niger*. These authors also revealed that melanized fungi could absorb heat from solar radiation in winter. Thus, dark-colored, many-celled conidia carry out both dispersal and resting functions, which is crucial in climatically and microclimatically stressful desert habitats.

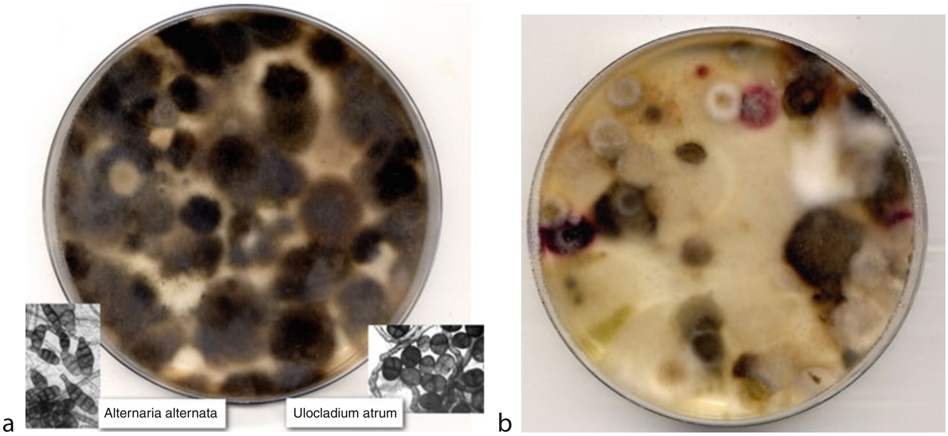

Fig. 10.2.1

Microfungal communities from crust (0–0.2 cm; a) and below soil layer (0.2–5 cm; b) in Nahal Nizana, the central Negev desert, Israel

Vertical distribution of microfungi through soil depth in a desert can efficiently illustrate the association between solar radiation and structure of microfungal communities. *Fig. 10.2.1* shows Petri dish cultures of microfungal communities from the soil layers 0–0.2 cm and 0.2–5 cm (a and b, respectively) sampled in Nahal Nizana, the central Negev desert. Communities from the uppermost crust layer are overwhelmingly dominated by melanin-containing fungi with many-celled conidia (*U. atrum*, *A. alternata*, *Embellisia phragmospora*, and *Stemphyllium* state of *Pleospora tarda*), while the layer only 0.2 cm below is mainly inhabited by light-colored species from the genera *Aspergillus*, *Penicillium*, *Fusarium*, and *Mortierella*.

Melanin-containing fungi prevailed also in the uppermost soil layer of the sunny-exposed south-facing slopes of the canyons located in northern Israel (Grishkan et al. 2003a) but quantitatively, this prevalence was almost two times less pronounced than in the desert and was subjected to seasonal changes (did not appear in the autumn and winter). Qualitatively, the group of melanized fungi in the northern canyons was mainly composed of species with one-celled, comparatively small conidia such as *A. niger*, *C. cladosporioides*, and *Humicola fuscoatra*. For *A. niger* from the Mount Carmel canyon, the concentration of melanin in conidia and their survival after UV-A exposure were examined in comparison between strains collected from the south-facing (SFS) and north-facing (NFS) slopes (Singaravelan et al. 2008). Conidia of the SFS strains contained melanin concentrations more than three-fold higher compared with conidia of the NFS strains. Such remarkable difference between slopes in melanin concentration was accompanied by significant difference in conidial culturability after UV-A irradiation and corresponded to the interslope microclimatic divergence caused by much higher solar radiation (200–800%; Pavlicek et al. 2003), which the SFS received in comparison with the NFS.

The effect of UV radiation has been also tested on the growth of Antarctic litter fungi (Hughes et al. 2003). Expectedly, hyphal extension rate of the melanin-containing *Phoma herbarum* was 2.5- to sixfold less reduced after the UV-B exposure than that of the light-colored species. *P. herbarum* produced a brown pigment within 24 h of the artificial UV treatment accompanied by production of fruit bodies and conidia. Key confirmation of the UV-protective role of black pigmentation has been obtained in studies that compared sensitivity of melanized and non-melanized strains of the same fungal species (e.g., Lamb et al. 1992; Rehnstrom and Free 1997). One of these studies was done on the coprophilous fungi *Ascobolus immersus*, *Sordaria brevicaullis*, and *S. fimicola* (Lamb et al. 1992). The authors tested UV-C sensitivity of the wild-type red or black pigmented ascospores of the fungi versus mutants with pale or no visible ascospore pigmentation thus avoiding complications associated with coevolutionary changes in efficiencies of repair mechanisms when comparing wild-types of different species. The experiment demonstrated direct association of UV-tolerance of the ascospores with the intensity of their dark pigmentation. It also revealed the importance of pigment distribution because the concentration of most of the red pigment into large granules in the *Ascobulus* mutant increased its UV-sensitivity although the total amount of pigment per ascospore was approximately the same as in wild-type.

Response to Ionizing Radiation

Radionuclide contamination as a source of ionizing radiation coming from exploitation of nuclear power plants, nuclear weapons, and uses of radioisotopes has become a reality nowadays and recent studies have demonstrated that fungi could be remarkably resistant to such kind of radiation. Resistance of many fungi, especially of melanized ones to gamma radiation was found to be higher than resistance of bacteria (➔ *Table 10.2.1*). Some melanin-containing fungi

Table 10.2.1

Comparative sensitivity of bacteria and fungi to external gamma radiation (adapted from Dadachova and Casadevall 2008)

Species	LD_{10} (kGy)[a]	Source
Bacteria		
Thermus thermophilis	0.8	Sghaier et al. 2008
Escherichia coli	0.7	Sghaier et al. 2008
Kineococcus radiotolerans	2	Sghaier et al. 2008
Rubrobacter xylanophilus	5.5	Sghaier et al. 2008
Deinococcus radiodurans	2–15	Sghaier et al. 2008
Fungi		
Penicillium lutum 352	0.4	Mirchink et al. 1972
Fusarium sp. 117	0.45	Mirchink et al. 1972
Stemphylium botryosum	>5	Mirchink et al. 1972
Alternaria tenuis	>5	Mirchink et al. 1972
Cladosporium cladosporioides	>5	Mirchink et al. 1972
Cryptococcus neoformans	4.3	Dadachova et al. 2004
Histoplasma capsulatum	6.7	Dadachova et al. 2004

[a] Dose (kilogray) required achieving 90% cell killing.

Note: ionizing radiation resistant bacteria (IRRB) are underlined; melanized fungi are in bold.

causing spoilage of food products (*A. alternata*, *Curvularia lunata*, and *C. genticulata*) were shown to survive under doses of gamma radiation exceeding the international standard for food (Saleh et al. 1988). Resistance of these fungi to the irradiation from a ^{137}Cs source was two- to eightfold higher than of the light-colored species involved in the experiment.

Measuring the rate of radionuclide immobilization by fungi indicated that dark-colored species had some advantage in this ability in comparison with light-colored ones. For example, mycelia of light pigmented fungi accumulated 1.1–4.7 less ^{90}Sr than mycelia of dematiaceous fungi (Zhdanova et al. 1990). Fully melanized *A. alternata* showed a higher capacity in uptake of both ^{60}Co and ^{137}Cs than *A. pulverulens* or *Fusarium verticilloides* (Mahmoud 2004). According to this author, melanin accounted for 45–60% of the incorporation of these isotopes into fungal hyphae.

Special attention was drawn to the resistance of fungi to ionizing radiation after the nuclear reactor accident at Chernobyl in 1986. Before the accident, soils in the Kiev region were dominated by non-melanized fungal genera, but after the radionuclide contamination in the vicinity of the reactor, these genera were replaced by melanin-containing genera such as *Stachybotrys*, *Ulocladium*, *Sporormiella*, *Humicola*, *Aureobasidium*, and *Alternaria* (Zhdanova et al. 2005). Comparison of the species growing under severe and comparatively weak radioactive pollution in the inner locations of the fourth unit of the Chernobyl nuclear power plant showed dominance of melanized fungi (mostly *Cladosporium* spp., *A. alternata*, and *A. pululans*) in heavily contaminated sites (Zhdanova et al. 2000). Some strains of *C. cladosporioides* and *C. sphaerospermum*, together with *Penicillium roseopurpureum* and *P. hirsutum*, isolated from the inner and outer locations of the reactor, displayed positive radiotropism, that is, statistically significant directed growth to the ^{109}Cd source of radiation (Zhdanova et al. 2004). The authors consider such fungi as promising bioremediation agents in radio-contaminated environments (Zhdanova et al. 2005).

Mechanism of Radioprotective Ability of Fungal Melanins

Amorphous semiconductivity of melanin (dihydroxyphenylalanine – DOPA – melanin), which forms free radicals and is itself a stable free radical, is considered to be the fundamental molecular property associated with the melanin radioprotective capacity (Hill 1992). DOPA melanin is able to convert different kinds of energy into vibrational and rotational activity in the melanin molecular structure dispersing it as heat and thus protecting a cell from the damaging effects of radiation (Butler and Day 1998). This energy absorbing and dispersing property accompanied with an ability to act as a sponge for cytotoxic free radicals was stated to be the fundamental explanation of melanin-protective functions.

The above explanations have been successfully confirmed in the experimental studies conducted by Dadachova et al. (2007a, b) that are discussed in detail by Dadachova and Casadell in ➋ Chap. 10.3 Melanin and Resistance to Ionizing Radiation in Fungi.

Other Functions of Fungal Melanins

While this chapter is devoted to the radioprotective function of fungal melanins, there are several other functions that are necessary for fungi in coping with environmental stress and thus are worth mentioning. Melanin can protect fungi against temperature extremes as it was shown on conidia of *Monilia fruticola* (heat) (Rehnstrom and Free 1997) and on *Cryptococcus neoformans* (both heat and cold) (Rosas and Casadevall 1997). Melanin probably prevents fungal cells from dehydration (Zhdanova and Pokhodenko 1973; Rehnstrom and Free 1997) because of its water-binding capacity (Prota 1992). Both these protective functions participate in overwhelming dominance of melanin-containing fungi on leaf surfaces and in the upper layers of desert soils as well as in highly saline environments (e.g., Gunde-Cimerman et al. 2004) even if they are slightly or non-UV-radiated (Grishkan et al. 2003b, 2004). Melanin is known to protect fungal cells not only from abiotic stress factors but also against enzymatic lysis by antagonistic microorganisms (e.g., Bull 1970; Old and Robertson 1970; Rehnstrom and Free 1997; Butler and Day 1998). Recently in the Netherlands, the proportion of melanized hyphae in different soil types was found to average 61% with highest values in non-disturbed forest soils where melanized hyphae actively participated in the degradation of recalcitrant organic substrates (van de Wal et al. 2009).

It has been found that melanin-containing microfungi increase their contribution to soil mycobiota in the response to chemical pollution (Marfenina 1998), especially near the roadsides both in soil and in winter snow cover (Kul'ko and Marfenina 2001). There is also evidence that melanin serves as a virulence factor contributing to fungal pathogenicity both for plants and animals (e.g., reviewed in Butler and Day 1998). Regarding the human pathogens *C. neoformans* and *Histoplasma capsulatum*, it has been shown that melanin protected fungal cells against microbicidal agents produced by immune effector cells (Wang and Casadevall 1994) as well as reduced the susceptibility of pigmented cells to antifungal drugs (Van Diun et al. 2002). In some plant pathogens, melanin is involved in penetration of appressoria into host cells by developing sufficient turgor pressure (Money and Howard 1996).

Fungal melanins have a high biosorptive capacity for a variety of metal ions (Fogarty and Tobin 1996, and references therein). The pigments can prevent toxic metals entering into the fungal cell. Adsorption of metal ions by melanized outer surfaces may also protect fungal propagules from antagonistic microorganisms (Rizzo et al. 1992). On the other hand, melanin was found to play a major role in the metal ion absorption in rock-inhabiting fungal microcolonies (Gadd and Mowll 1985). Such binding capacity might be especially important on rock surfaces in providing fungi with necessary ions and stimulating their growth and survival (Gorbushina et al. 2002).

Conclusion

Melanin is not a necessary compound for fungal growth because both pigmented and non-pigmented strains of the same fungus can exist. But as a huge quantity of evidence from nature and laboratory experiments testify, this pigment is highly advantageous for fungi in withstanding various environmental extremes. The ability to absorb all types of electromagnetic radiation is an important feature of melanin which bestows the pigment with the capacity for both energy transformation and shielding. The well-established fact that melanin-containing fungi as well as other melanized organisms inhabit highly radiated environments all over the world, together with phenomenon of "radiotropism" has prompted the conclusion that melanin probably has functions analogous to other energy-harvesting pigments such as chlorophyll (Dadachova and Casadevall 2008).

Cross-References

- 3.3 Osmoadaptation in Methanogenic Archaea: Physiology, Genetics, and Regulation in *Methanosarcina mazei* Gö1
- 6.4 Adaptation Mechanisms of Psychrotolerant Bacterial Pathogens
- 10.1 *Deinococcus radiodurans*: Revising the Molecular Basis for Radiation Effects on Cells

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