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RESEARCH ARTICLE

Molecular and physiological effects of environmental UV radiation on fungal conidia

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Abstract Conidia are specialized structures produced at the end of the asexual life cycle of most filamentous fungi. They are responsible for fungal dispersal and environmental persistence. In pathogenic species, they are also involved in host recognition and infection. Conidial production, survival, dispersal, germination, pathogenicity and virulence can be strongly influenced by exposure to solar radiation, although its effects are diverse and often species dependent. UV radiation is the most harmful and mutagenic waveband of the solar spectrum. Direct exposure to solar radiation for a few hours can kill conidia of most fungal species. Conidia are killed both by solar UV-A and UV-B radiation. In addition to killing conidia, which limits the size of the fungal population and its dispersion, exposures to sublethal doses of UV radiation can reduce conidial germination speed and virulence. The focus of this review is to provide an overview of the effects of solar radiation on conidia and on the major systems involved in protection from and repair of damage induced by solar UV radiation. The efforts that have been made to obtain strains of fungi of interest such as entomopathogens more tolerant to solar radiation will also be reviewed.

Keywords Fungal photobiology · UV tolerance · UV-induced damage · Microbial sunscreens · Conidia · Plant-pathogenic fungi · Insect-pathogenic fungi

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Introduction

Most of the studies that evaluated the effects of UV radiation on fungi were conducted with conidia because, besides being biologically important, they are also more easily produced and manipulated than mycelia (Braga et al. 2001a, b, c, d, 2006; Rangel et al. 2006a, b; Luque et al. 2012; de Menezes et al. 2014a, b, 2015). Conidial production, survival, dispersion, distribution, germination, pathogenicity, and virulence can be strongly influenced by exposure to solar radiation, although its effects are diverse and often species dependent (Rotem et al. 1985; Paul et al. 1997; Newsham et al. 1997; Braga et al. 2001a, b, c, d; Englander et al. 2006; Fourtouni et al. 1998; Fernandes et al. 2007; Corrochano and Garre 2010;

Nascimento et al. 2010; Santos et al. 2011; Idnurm 2013; Cheng et al. 2014).

Due to the correlation between different wavebands in the solar spectrum, exposures to solar radiation are directly related to the increase in temperature, dehydration, and UV-induced damage in most organisms (Rotem et al. 1985; Wu et al. 2000; Mizubuti et al. 2000; Braga et al. 2001d; Ningen et al. 2005; Nascimento et al. 2010). The UV region of the solar spectrum constitutes only a minor proportion of the sunlight that reaches the Earth's surface. However, its effects are disproportionately large, because UV photons can be absorbed by several biomolecules, which results in cellular photodamage (Nascimento et al. 2010; Gao and Garcia-Pichel 2011). UV radiation is the most harmful solar waveband for fungi, as demonstrated by the evaluation of action spectra for various species (Maddison and Manners 1973; Paul et al. 1997). The ultraviolet spectrum is conventionally divided into three wavelength intervals: UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (100–280 nm) (Coblentz 1932). Today, however, many reports use 320 nm as the division between the UV-A and UV-B wavebands. Only UV-A and UV-B radiation reach the Earth's surface, because atmospheric ozone drastically reduces the penetration of radiation with wavelengths shorter than 320 nm and completely excludes those below 290 nm (Caldwell and Flint 1997). In quantitative terms, UV-A is responsible for approximately 95 % of the total energy of the UV spectrum that reaches the Earth's surface and UV-B is responsible for the remaining 5 % (Christiaens et al. 2011; Schuch et al. 2012). Nevertheless, the high biological effects of UV-B are important despite its reduced penetration of the Earth's atmosphere.

Solar UV radiation, and especially UV-B, varies considerably over the Earth's surface, being more intense at lower latitudes, higher elevations, and in areas with fewer clouds [see global illustration in McKenzie et al. (2007)]. While stratospheric ozone levels are critical in determining ground-level UV radiation, the limitations on emission of ozone-depleting substances specified by the Montreal Protocol have prevented cataclysmic ozone depletion (Newman and McKenzie 2011). Ozone recovery, however, has yet to show significant decreases in UV-B radiation (Bais et al. 2015). Air pollution (including aerosols) has a substantial effect on ground-level UV radiation. Substantial increases in UV radiation are anticipated in populated areas of the northern hemisphere if air quality improves (Bais et al. 2015).

Fungi react to solar radiation in different ways, and the effects of the radiation depend on the wavelength and irradiance of the incident photons that strike the cells (Paul et al. 1997; Fuller et al. 2013, 2015). Exposure to moderate irradiances of visible light (400–700 nm) and near-UV radiation stimulates conidial production, synthesis of photoprotective pigments, and secondary metabolites in several fungal species (Leach and Tulloch 1972; Alves et al. 1984; Mooney and Yager 1990; Fourtouni et al. 1998; Zhang et al. 2009; Avalos and Estrada 2010; Röhrig et al. 2013; Fuller et al. 2013; Olmedo et al. 2013; de Menezes et al. 2015). Light exposure can also pre-adapt fungal structures such as conidia and mycelia to forthcoming stresses (Rangel et al. 2011; Verma and Idnurm 2013; Fuller et al. 2013; de Menezes et al. 2015). There are also links between light-sensing and fungal pathogenicity and virulence in animal- and plant-pathogenic fungi (Hammerschmidt and Nicholson 1977; Ravid and Antignus 2004; Ruiz-Roldán et al. 2008; Idnurm et al. 2010; Idnurm 2013; Yu et al. 2013; Cheng et al. 2014).

Among the main selective pressures that drive the perception of solar radiation by fungi is the protection against damage induced by UV radiation (Purschwitz et al. 2006; Corrochano and Garre 2010; Idnurm et al. 2010; Verma and Idnurm 2013). The detrimental effects of solar radiation limits survival and dispersal of important plant- and animal-pathogenic fungi; this represents a serious impediment to the use of fungi, such as entomopathogens and mycopathogens, in biological control programs (Costa et al. 2012; Braga et al. 2001a, b, c, d). A few hours of exposure to solar radiation can kill unprotected conidia of most fungal species (Rotem et al. 1985; Wu et al. 2000; Mizubuti et al. 2000; Braga et al. 2001a, b, c, d; Rangel et al. 2006a; Fernandes et al. 2007). In addition to killing conidia, exposures to sublethal fluences of UV radiation can reduce conidial germination speed and virulence (Rasanayagam et al. 1995; Paul et al. 1997; Nascimento et al. 2010; Cheng et al. 2014).

In fungi, the selective pressure from solar radiation has resulted in their acquiring a series of mechanisms for protection against solar UV radiation. As in all living beings, fungal tolerance to solar radiation is a quantitative trait determined both by protective mechanisms that prevent or reduce the occurrence of damage to intracellular components, and by several systems that repair the damage caused by radiation (Chelico et al. 2006; Rangel et al. 2006a; Braga et al. 2006; Chelico and Khachatourians 2008; Nascimento et al. 2010). The actions of these mechanisms sometimes partially overlap. Among the major protective systems are pigments such as melanins and melanin-like compounds located in the cell wall and cytoplasmic small colorless UV-absorbing metabolites that act as sunscreens (Blanc et al. 1976; Al-Rubeai and El-Hassi 1986; Rangel et al. 2006a; Braga et al. 2006; Schiave et al. 2009; Nascimento et al. 2010; Carollo et al. 2010) and also enzymes and metabolites that can inactivate reactive oxygen species induced by solar UV radiation (Miller et al. 2004; Solomon et al. 2007; Wang et al. 2012; Avalos and Limón 2015). Among the several DNA repair mechanisms described in fungi, nucleotide excision repair (NER) and photoreactivation (PR) are important in the repair of UV-induced damage (Goldman and Kafer 2004; Chelico et al. 2005, 2006; Chelico and Khachatourians 2008; Fang and St. Leger 2012).

We will review the effects of solar radiation and the major systems involved in the protection and repair of damage induced by solar UV radiation in conidia and germlings. The efforts that have been made to produce fungi more tolerant to solar radiation and, therefore, more efficacious as biological control agents will also be presented.

Light sources, filtering lamps and sunlight, measuring irradiance, and selecting biological weighting factors (action spectra)

Sunlight, like most natural phenomena, includes an extremely variable set of conditions. The most important of these are intensity and spectral content. Both of these parameters vary due to season, time of the day, location, altitude, and atmospheric conditions (McKenzie et al. 2007; Christiaens et al. 2011; Schuch et al. 2012). Due to the uncontrollable circumstances associated with working outdoors, most studies on the effects of solar radiation on fungi are performed in the laboratory. This leads to one of the central methodological questions of solar UV research, namely, how do we obtain realistic fluences (light doses) of the wavelengths in solar radiation that cause both damage and repair, and how do we reconcile the fluences, irradiances, and spectra used in the laboratory with what is present in nature? It is important to have knowledge of solar UV at the location of interest. The level of detail at which this should be pursued depends on the goals of the experiment. Models, which utilize a variety of input parameters, may be used to predict UV. They range from simple inputs [latitude, date, time (Diffey 2015)] to more complex, requiring also ozone thickness, surface albedo, and elevation (http://cprm.acd.ucar.edu/Models/TUV/Interactive_TUV/). In some locations, UV-monitoring networks are able to provide years of daily spectral irradiance measurements (e.g., http://uvb.nrel.colostate.edu/UVB/index.jsf). Ideally, spectral irradiance measurements (e.g., mW m^{-2} nm^{-1}) should be obtained to calculate spectral weighting functions (described below). Typically, UV climatologies are less useful for fungal work as they often have UV radiation weighted for other effects, such as human erythema. Combinations of lamps and filters are then devised to attempt replication of the location of interest. Ideally, if planning to do field work in a specific area, one should take local spectral irradiance measurements in various seasons and at different times of the day.

Lamps are used in most of the reports on the effects of solar irradiation on fungi (Ignoffo and Garcia 1992; Morley-Davies et al. 1996; Fargues et al. 1996; Moody et al. 1999; Braga et al. 2001a, b, c, 2002, 2006; Nascimento et al. 2010; Luque et al. 2012; Wang et al. 2013). Nevertheless, lamps can only approximate the spectrum and intensity of bright sunlight. Fluorescent lamps can be used separately, in combinations of UV-B, UV-A, and visible light-emitting lamps, or combined with xenon lamps, which have high intensity and contain UV-A, UV-B, and visible light (Braga et al. 2006; Rangel et al. 2006a). Even with these sophisticated irradiation systems, UV-A levels are often considerably less than that found in nature. There are lamp/filter systems on the market designed specifically as "solar simulators". In general, these are based on reasonably potent (300–1600 watt) lamps. Their spectral output is somewhat similar to midday sunlight (although careful measurements should still be taken) and these instruments have been utilized in a number of research projects with good results (e.g., Alves et al. 1998), although the irradiated area is small. One obvious advantage of fluorescent lamps, besides low cost, is their vastly increased target area which allows simultaneous trials of a variety of strains or different times of exposure (Braga et al. 2001a, b, c, d, 2006; Rangel et al. 2006a).

Of key importance in all experiments with lamps is the elimination of all wavelengths below 290 nm, as these short wavelengths are absorbed in the atmosphere, primarily by ozone. The region of the spectrum below 280 nm is referred to as UV-C and includes the wavelengths emitted by germicidal lamps. The biological activity of these short wavelengths, particularly around 254 nm, is extremely high. If any of these short wavelengths are present, unrealistic levels of damage may result. Their elimination can be assured with several types of filters. For simulating sunlight, the most commonly used material is cellulose diacetate, which removes wavelengths shorter than 290 nm. Another type of film, clear polyester (e.g., Mylar), is routinely used to remove both UV-C and UV-B. This film has often been used to provide a UV-B-free control in experiments primarily examining ozone depletion. The removal of all UV (UV-A, UV-B, UV-C) can be accomplished with a Llumar film. The lower cutoff of Lumar is at about 400 nm. The use of this film will permit studies of visible wavelengths. These filters and others may be used in filtered-sunlight experiments (e.g., Braga et al. 2001d; de Menezes et al. 2014a, b). See Krizek et al. (2005) or Ryel et al. (2010) for graphical depictions of various filter transmittances. Because these filters are often used for commercial purposes unrelated to their optical properties, it is best to verify their spectral transmittance with a spectrophotometer.

A complicating factor is that the response to UV irradiation is temperature dependent (Petin et al. 1997). Accordingly, laboratory experiments must be conducted in chambers with tight temperature control, and it is best to locate the different treatments in the same chamber. When conducting outdoor direct sunlight experiments, there can be tremendous heat buildup and, therefore, temperature control systems must be used. In our case, we have floated our

experiments on temperature-controlled water (Braga et al. 2001d; de Menezes et al. 2014a, b).

The most precise measurement of radiation, whether from lamps or sunlight, is performed with a spectroradiometer, which measures spectral irradiance (intensity at 1-nm intervals). We normally do this from 250 nm to at least 400 nm. Measurements from 250 to 290 nm are taken to assure that no wavelengths below 290 nm pass through the filter. Measurement of spectral irradiance allows the utilization of weighting formulas (discussed below) to compare the biological effectiveness of various treatments with what is found in nature. Time-integrated UV measurements, using inexpensive UV-absorbing polymers, may be an appropriate substitute in some field situations with variable or heterogeneous light (Parisi et al. 2010). Spectroradiometers and other broadband radiometers currently available vary greatly in their cost and technical specifications. An analysis of the various options available (e.g., Aphalo et al. 2012) should be made to determine the appropriate UV-measuring instrument for the type of experiment planned. Biological spectral weighting functions (BSWFs), often derived from action spectra, are usually employed to permit a basis for comparison between various irradiation systems and sunlight. These functions are used to scale the relative biological effectiveness of each wavelength. By convention, these factors are normalized to one at 300 nm. Multiplying the weighting factors by the spectral irradiance produces an integrated "biologically effective UV irradiance", UV_{BE}. Ultraviolet action spectra have been published for many fungal responses such as stimulation of conidiogenesis in *Pleospora herbarum*, *Alternaria dauci*, *Stemphylium solani*, and *Botrytis cinera* (Honda and Yunoki 1978), stimulation of perithecial formation in *P. Herbarum* (Leach and Trione 1966; Sproston 1971; Leach 1972), and inhibition of germination of *Puccinia striiformis* and *Puccinia graminis* uredospores (Maddison and Manners 1973). Several of these BSWFs differ considerably from each other. Consequently, selection of the most appropriate spectral weighting function is critical, and this selection has profound effects on the outcome of the experiment (Paul et al. 1997, 2005; Flint and Caldwell 2003; Braga et al. 2006).

Unfortunately, there is often little information available for guidance in selecting weighting functions. Most are derived from laboratory experiments with monochromatic or narrowband radiation and are usually conducted without the wavelengths that induce repair mechanisms. Thus, if possible, the appropriateness of different weighting functions should be evaluated under realistic conditions (sunlight). For our work with the entomopathogen *Metarhizium* ssp., there was little precedent in the recent literature for a spectral weighting function pertinent to the conidial killing or inhibition of its germination. We followed a recommendation of Paul et al. (1997): the average response of nine fungal spectra (which had been derived decades earlier) corresponded closely with the action spectra for DNA damage in plant seedlings (Quaite et al. 1992). We have been using this plant DNA damage weighting function with entomopathogenic fungi such as *Metarhizium robertsii*, *M. anisopliae*, *M. acridum*, *M. guizhouense*, *M. flavoviride*, *M. globosum* (Braga et al. 2001a, b, c, d, 2002, 2006; Nascimento et al. 2010), *Verticillium lecanii* (now: *Simplicillium lanosoniveum*), and *Aphanocladium album* (now: *Lecanicillium aphanocladii*) (Braga et al. 2002), plant pathogens such as *Colletotrichum acutatum* and *C. gloesporioides* (de Menezes et al. 2014a, b, 2015), saprophytes such as *A. nidulans* (Nascimento et al. 2010), and opportunistic human pathogens such as *Aspergillus fumigatus* (Nascimento et al. 2010), *Cryptococcus neoformans*, and *C. laurentii* (Schiave et al. 2009). Data from a field experiment conducted with *M. robertsii* and *M. acridum* conidia suggest that a BSWF that gives greater emphasis to UV-A than the Quaite DNA-damage formula may be more appropriate, at least for the study of the detrimental effect of solar UV on conidia, such as killing and delay in germination (Braga et al. 2001d). This may be true for some other fungal species as well (Paul et al. 2005, 2012).

Overview of UV-induced damage

The nature of the DNA damage induced by UV radiation strongly depends on the wavelength of the incident photons (Kielbassa et al. 1997; Douki et al. 2003; Schuch et al. 2009; Cadet et al. 2012; Karentz 2015). UV-induced damage to cellular DNA can arise either from a direct photoreaction triggered by the absorption of UV-B or UV-A photons or by photosensitization. In the latter case, the mechanism may involve excitation of endogenous chromophores with subsequent conversion to long-lived excited triplet states by intersystem crossing (Kielbassa et al. 1997; Cadet et al. 2012, 2015). The direct UV-B radiation absorption by DNA results mainly in dimerization between adjacent pyrimidine bases. Cyclobutane pyrimidine dimers (CPDs) and pyrimidine (6-4)-pyrimidone photoproducts (6-4PPs) are the two main categories of bipyrimidine photoproducts induced by UV-B radiation (Chelico and Khachatourians 2008; Schuch et al. 2009; Nascimento et al. 2010; Cadet et al. 2012). CPDs arise from a [2+2] cycloaddition reaction between the C5–C6 double bonds of two pyrimidines. 6-4PPs are produced by a [2+2] cycloaddition between the C5–C6 double bond of the 5′-end base and the C4 carbonyl group of a 3′-end thymine (Cadet et al. 2012). UV-B radiation also induces oxidative degradation pathways (Cadet et al. 2015). The formation of oxidation products, more specifically 8-oxo-7,8-dihydro-2′-deoxyguanosine (8-oxodGuo), is also induced by UV-B,

however, in a low yield that is two to three orders of magnitude lower than of either CPDs or 6-4PPs (Cadet et al. 2012).

UV-A constitutes a large part of solar UV radiation, but it is evident that UV-A radiation is far less efficient in producing direct photo-lesions than UV-B (Schuch et al. 2009; Cadet et al. 2012, 2015). Like UV-B, UV-A also induces the formation of bipyrimidine photoproducts, although much less efficiently and through a mechanism different from that triggered by UV-B (Douki et al. 2003; Schuch et al. 2009). Bipyrimidine photoproducts are the main type of DNA damage involved in the genotoxic effect of solar UV-A radiation in mammalian cells (Douki et al. 2003; Mouret et al. 2006). In contrast to UV-B, UV-A generates CPD with a large predominance of TT CPDs. Cyclobutadithymine (T<>T) is formed in UV-A irradiated cellular DNA according to a direct excitation mechanism with a higher efficiency than oxidatively generated DNA damage that arises mostly through the type II photosensitization mechanism (Banyasz et al. 2011; Cadet et al. 2012, 2015). Oxidatively generated DNA damage is more effectively induced with UV-A than UV-B (Schuch and Menck 2010; Cadet et al. 2015). Oxidized purine bases and most likely 8-oxo-7,8-dihydroguanine (8-oxoGua) are the main UVA-induced oxidation products in UV-A irradiated cells (Douki et al. 2003; Schuch et al. 2009). The second most frequent UV-A-induced DNA oxidatively generated lesions are strand breaks that are formed in an approximately three times lower yield than oxidized purines (Cadet et al. 2012). Oxidized pyrimidines also occur, but at levels of less than half of strand breaks (Cadet et al. 2012). The distribution of the UV-A-induced DNA oxidation products depends both on the cell type and on the wavelength of the incident UV-A photon (Cadet et al. 2012).

Conidial structure

In contrast to vegetative mycelium, which has high metabolic activity, conidia of most fungi are dormant or quiescent structures (Bonnen and Brambl 1983; Van Etten et al. 1983; Schadeck et al. 1998; Braga et al. 1999). Processes such as transcription and protein synthesis normally do not occur in mature conidia until germination, limiting their physiological adaptation and response to environmental changes (Bonnen and Brambl 1983; St. Leger et al. 1989a, b; d'Enfert 1997; Osherov and May 2000). Conidia also differ from the vegetative cells, both in their transcriptome and proteome (St. Leger et al. 1989a, b; Lamarre et al. 2008; Barros et al. 2010; Oh et al. 2010). We have established conidial and mycelial proteome reference maps for *M. acridum*. In all, 1130 and 1200 protein spots were detected in ungerminated conidia and fast-growing mycelia, respectively. Comparison of the two protein expression profiles revealed that only 35 % of the protein spots were common to both developmental stages (Barros et al. 2010). The overrepresented proteins in *A. fumigatus* and *M. acridum* resting conidia compared to mycelium included stress-protector proteins such as heat shock proteins (HSP) and proteins involved in reactive oxygen intermediate detoxification and pigment biosynthesis (Barros et al. 2010; Wang et al. 2013). The presence of pre-existing mRNAs and proteins in conidia is presumably required for their tolerance to environmental stresses and ability to immediately resume the numerous metabolic activities in response to an environmental stimulus (St. Leger et al. 1989b; Cooper et al. 2006; Lamarre et al. 2008; Noir et al. 2009; Barros et al. 2010; Oh et al. 2010). Conidia also accumulate melanins, carotenoids, and other pigments (Claverie-Martin et al. 1988; Rangel et al. 2006a; Braga et al. 2006; Pihet et al. 2009; Nascimento et al. 2010; Avalos and Limón 2015) and several secondary small metabolites, including UV-absorbing compounds that are not present in mycelia (Carollo et al. 2010; Keller 2011). Secondary metabolite production is correlated with conidial development in numerous fungi (Calvo et al. 2002).

Conidial protection against UV radiation

Many fungi are exposed to solar radiation and high temperatures during part of their life cycle. The deleterious effects of solar radiation and heat have led fungi to develop a series of defense systems. The genetic basis of cellular tolerance to solar radiation is multifactorial and involves (a) pigments, such as melanins, located in the cell wall, and endogenous or extracellular non-chromogenic UV-absorbing metabolites that act as sunscreens (Braga et al. 2006; Rangel et al. 2006a; Schiave et al. 2009; Carollo et al. 2010); (b) enzymes, such as catalases, SODs, and peroxidases and non-enzymatic antioxidants, such as carotenoids and reduced glutathione that can inactivate the toxic reactive oxygen species induced by UV radiation (Miller et al. 2004; Soriani et al. 2009; Xie et al. 2012; Avalos and Limón 2015); (c) cellular metabolites, such as polyols that mitigate the effects of the radiation (Rangel et al. 2008, 2005a, b, c); and (d) DNA repair systems capable of repairing the damage induced by radiation. Among the several DNA repair mechanisms described in fungi, nucleotide excision repair (NER) and photoreactivation (PR) are important in repairing UV-induced damage (Goldman and Kafer 2004; Chelico et al. 2005, 2006; Berrocal-Tito et al. 2007; Bayram et al. 2008; Chelico and Khachatourians 2008; Fang and St. Leger 2012).

Conidial sunscreens

According to Gao and Garcia-Pichel (2011), to be considered a microbial UV sunscreen, a compound should absorb in the UV range with a high absorption coefficient and be present at concentrations sufficient to cause a substantial reduction in the UV dose received by the microbial cell. It cannot act as a photosensitizer and should dissipate the absorbed energy without damaging the cell. Sunscreens usually accumulate specifically at sensitive fungal life cycle stages and/or are induced by exposure to solar radiation (Kihara et al. 2004a, b; Braga et al. 2006; Rangel et al. 2006a; Avalos and Limón 2015; de Menezes et al. 2015). Additionally, because sunscreens act as a passive defense mechanism shielding the cell from incoming radiation, UV protection should be achieved in physiologically inactive structures such as conidia (Braga et al. 2006; Rangel et al. 2006a; Gao and Garcia-Pichel 2011).

Conidia of different species accumulate several characterized and non-characterized pigments, including melanins and melanin-like pigments that may act as sunscreens. Melanins are dark pigmented multifunctional polymers composed of various types of phenolic or indolic monomers, usually complexed with proteins, and often with carbohydrates (Butler and Day 1998). Usually, they are synthesized during conidia formation for deposition in the cell wall (Calvo et al. 2002; Pihet et al. 2009). Melanins are multifunctional and protect fungi against environmental stresses such as solar radiation, oxidizing agents, and ionizing radiation (Gonçalves and Pombeiro-Sponchiado 2005; Dadachova et al. 2008; Eisenman and Casadevall 2012). Even after several decades of intensive study, the detailed chemical structure of melanins remains unknown.

The biosynthetic pathways for several different fungal melanins are known, with the two best characterized being the 1,8-dihydroxynaphthalene (DHN) pathway and L-3,4-dihydroxyphenylalanine (L-DOPA) pathway (Butler and Day 1998; Henson et al. 1999; Schiave et al. 2009; Eisenman and Casadevall 2012; Rodrigues et al. 2012). In L-DOPA melanin synthesis, the precursor (L-DOPA or tyrosine) is catalyzed by tyrosinase or catalase into dopaquinone, which is converted into dihydroxyindole for polymerization into melanin (Chen et al. 2015). Many if not all filamentous melanogenic fungi synthesize melanin via the DHN pathway (Butler and Day 1998). In this pathway, the precursor molecule, acetyl coenzyme A or manolyl coA, is produced endogenously. The first step, formation of 1,3,6,8-tetrahydroxynaphthalene (1,3,6,8-THN), is catalyzed by a type I polyketide synthase (PKS). A hydroxynaphthalene reductase converts 1,3,6,8-THN to scytalone. Dehydration of scytalone by scytalone dehydratase results in 1,3,8-trihydroxynaphthalene (1,3,8-THN). 1,3,8-THN reductase converts the 1,3,8-THN to vermelone, which is further dehydrated to 1,8-DHN. Finally, oxidative polymerization of 1,8-DHN gives DHN melanin (Butler and Day 1998). Genetic sequencing and genetic complementation studies have shown that DHN melanin pathways are functionally comparable in several fungi, including *Magnaporthe grisea*, *Alternaria alternata*, *Colletotrichum lagenarium*, *Cochliobolus heterostrophus*, and *Aspergillus* spp. (Henson et al. 1999). The intermediates and autooxidation products of DHN melanin pathway can be obtained from mutants or by inhibitor studies (Butler and Day 1998; Kihara et al. 2004a, b, 2008). In some cases, the specific inhibition of a melanin synthesis pathway by a chemical came to be regarded as sufficient proof that a substance was melanin. A black or near black fungal pigment was characterized as a DHN melanin when its biosynthesis was specifically inhibited by the systemic fungicide tricyclazole. Pathway catalytic mechanism and inhibitors are discussed in detail by Butler and Day (1998). Several reviews covering different aspects of fungal melanins are available (Henson et al. 1999; Butler et al. 2001; Eisenman and Casadevall 2012).

Melanins and melanin-like pigments have been linked to conidial tolerance to solar radiation and other environmental stresses in several fungal species (Butler and Day 1998; Kihara et al. 2004a, b, 2008; Singaravelan et al. 2008; Tseng et al. 2011; Eisenman and Casadevall 2012). Usually, they are located outside the plasma membrane and seem to be an important structural component of conidia cell wall (Pihet et al. 2009). The molecular and genetic basis of conidial pigmentation has been studied in several species. Melanogenesis in fungi varies among species, from constitutive to developmentally regulated, in which case pigmentation is typical of aerial mycelia and conidia (Kihara et al. 2008; Gao and Garcia-Pichel 2011). Expression of three genes involved in melanin biosynthesis, polyketide synthase gene, scytalone dehydratase gene, and 1,3,8-THN reductase gene, is specifically up-regulated by near-UV (300–400 nm) radiation in the phytopathogenic fungus *Bipolaris oryzae* (Kihara et al. 2004a, b). Kihara et al. (2008) isolated and characterized *Bipolaris* melanin regulation gene (*BMR1*) encoding a transcription factor for melanin biosynthesis genes in *B. oryzae*. The expression of the *BMR1* gene was significantly enhanced in mycelia exposed to near UV, which suggests that the near-UV radiation-enhanced *BMR1* expression would lead to accumulation of the Bmr1 transcription factor, resulting in up-regulation of the three melanin biosynthesis genes under near-UV radiation (Kihara et al. 2008). Melanin accumulation in conidia of *A. niger* is an adaptive trait against solar UV radiation generated by natural selection (Singaravelan et al. 2008).

Fungi of the genera *Aspergillus* and *Metarhizium* produce greenish conidia. The olive-green coloration may

arise when melanin-like pigments are complexed with proteins and other compounds (Ray and Eakin 1975; Butler et al. 2001). The biosynthesis of melanin-like pigments has been detected during conidiation in fungi with greenish (*A. nidulans*) (Adams et al. 1998) and bluish-green (*A. fumigatus*) (Tsai et al. 1998, 1999) conidia. *A. fumigatus* conidia are known to produce greenish pigments by using the DHN melanin pathway (Wheeler and Bell 1988). Wild *Metarhizium* spp. isolates have dark-green conidia, with the green tonality varying widely among isolates. The chemical identity and the synthesis pathway of the greenish pigment in *Metarhizium* conidia are still unknown, but the synthesis of the green conidial color seems to depend on at least two different metabolic pathways as in *A. niger* (Ray and Eakin 1975; Magoon and Messing-Al-Aidroos 1985). Four loci involved in *A. niger* conidial pigmentation were identified (Jørgensen et al. 2011). The DHN melanin synthesis pathway is absent in *M. robertsii*, because the fungus lacks scytalone dehydratase activity (a central enzyme in this pathway) (Rangel et al. 2006a). The DHN melanin inhibitors pyroquilon and tricyclazole did not impair conidial colorization in this fungus (Rangel et al. 2006a; Chen et al. 2015). Kojic acid and glufosinate ammonium do not inhibit conidial color formation either, suggesting that DOPA melanin and carotenoids pathways do not contribute to pigmentation in *M. robertsii* (Fang et al. 2010). Likewise, *Metarhizium* did not generate pyomelanin on medium containing L-tyrosine with or without sulcotrione, which suggests that it may not use the pyomelanin synthesis pathway (Fang et al. 2010). Together, these studies indicated that wild-type *Metarhizium* lacked the enzymatic machinery for DHN melanin synthesis and implies the presence of an unusual, yet undetermined, pathway(s) for pigmentation in this fungal genus. Two PKS (MrPks1 and MrPks2), which show modular and sequence similarities to functionally verified PKS enzymes involved in melanin/pigment biosynthesis, were reported in *M. robertsii* (Chen et al. 2015). Deletion of *MrPks1* but not *MrPks2* impaired conidial pigmentation in two different strains (ARSEF 2575 and ARSEF 23). Disruption of *MrPks1* resulted in a change in conidial color from dark green to reddish brown and reduced the tolerance to UV-C radiation in strain ARSEF 23, but not in strain ARSEF 2575. The results also suggested that the two genes are not involved in melanin biosynthesis in *M. robertsii* (Chen et al. 2015).

Fang et al. (2010) reported a class 1 laccase (MLAC1) involved in conidial pigmentation in *M. anisopliae*. *Mlac1* is expressed exclusively in the later stages of conidiation and in blastospores when *M. anisoplia* is living as a saprophyte. During infection processes, *Mlac1* is also expressed by appressoria. Disrupting *Mlac1* reduced virulence and produced a yellow-conidia phenotype with increased conidia susceptibility to UV-B radiation and heat shock.

Mutants with conidia of different colors were obtained from different *Metarhizium* species and strains by exposing the fungi to UV-B radiation (Braga et al. 2006; Rangel et al. 2006a). Although they are easily obtained in the laboratory, these color mutants are rarely found in nature, indicating that the wild conidial color is an important adaptive trait. We demonstrated the importance of pigmentation of *M. robertsii* conidia to tolerance against solar-simulated radiation (Braga et al. 2006; Rangel et al. 2006a). Mutants with white conidia were more sensitive to simulated solar UV radiation than purple mutants, which were more sensitive than yellow ones and in turn were more sensitive than the dark-green wild type. White conidia had a tenfold lower survival rate than the wild strain after exposure to UV fluence of 6.5 kJ m^{-2} (Quaite-weighted fluence). Three of the four purple mutants were quite similar in that they had less than half the tolerance of the wild-type strain. Of the five yellow mutants evaluated, three had significantly lower tolerance and two were close to that of the wild strain. The mutants identified as "yellow" showed a wide diversity of yellowish hues. A yellow and a purple mutant that were very sensitive to UV-B radiation were reverted to green conidia and both revertants exhibited wild-type UV-B tolerance (Braga et al. 2006). However, the importance of conidial pigmentation to UV-B tolerance varied among the different *M. robertsii* isolates (Rangel et al. 2006a).

We also demonstrated that the green pigment present in the wild-type strain could protect the DNA of the conidia against the mutagenic effect of solar radiation. The frequency of CPDs in an albino mutant was approximately ten times higher than of its green wild-type parent strain after exposure to a sublethal fluence (1.8 kJ m^{-2}) of UV_{BE} radiation, which explains, at least in part, the lower tolerance to solar radiation of the mutant. Despite the difference between the amounts of DNA damage, no proportional difference was observed between the germination delays of the wild-type and albino mutant. This discrepancy may be explained by the multifactorial nature of UV tolerance, which does not depend only on the amount of the DNA lesions (Nascimento et al. 2010). The protective role of melanin-like pigments against UV radiation was observed in conidia of other species. Conidia of *A. niger* mutants with white and fawn conidia were more sensitive to UV-C radiation than the wild type possessing a dark pigment (Esbelin et al. 2013). Albino teliospores of the basidiomycete *Ustilago nuda* are less tolerant to UV-C radiation and visible light than the wild type (Will III et al. 1987).

Other pigments and mycotoxins present in conidia have also been associated with tolerance to UV radiation. Aflatoxins are highly toxic and carcinogenic secondary metabolites produced primarily by *A. flavus* and *A. parasiticus* (Medina et al. 2015). Aflatoxins and some of their

precursor metabolites protect *Aspergillus* conidia against UV radiation. Conidia of isogenic mutants of *A. flavus* and *A. parasiticus*, lacking the ability to accumulate any aflatoxin precursor metabolite, are much less tolerant to UV-B than the aflatoxin-producing strains or pigmented mutants that accumulate aflatoxin precursors (Ehrlich et al. 2010). Størmer et al. (1998) suggested that the UV-absorbing mycotoxin citrinin present in the outer layers of conidia of *Penicillium verrucosum* could act as a sun protectant.

Carotenoids

Carotenoids are lipophilic terpenoid pigments that occur in fungi of several genera such as *Mucor*, *Phycomyces*, *Sclerotium*, *Sclerotinia*, *Ustilago*, *Aspergillus*, *Cercospora*, *Penicillium*, and *Aschersonia*, among others (Blanc et al. 1976; Luque et al. 2012; Avalos and Limón 2015). They contain an aliphatic polyene chain usually composed of eight isoprene units that include light-absorbing conjugate double bounds providing characteristic yellow, orange, or reddish colors (Avalos and Limón 2015).

The protective role of carotenoids against oxidative stress and exposure to UV radiation is supported by different lines of evidence (Avalos and Limón 2015; Gao and Garcia-Pichel 2011). The conjugated polyene chain of carotenoids provides chemical reactivity against oxidizing agents and free radicals. This makes the carotenoids efficient scavengers of singlet molecular oxygen and peroxyl radicals and permits the dissipation of the energy from photosensitizers (Avalos and Limón 2015). As most carotenoids absorb mainly in the visible region (>400 nm), their beneficial effects in UV radiation protection are probably due to their capacity to act as quenchers of photosensitization products and also as inhibitors of free-radical reactions (Gao and Garcia-Pichel 2011).

The protective role of carotenoids against oxygen singlet and other reactive oxygen species was demonstrated in *Neurospora crassa* conidia. Phenothiazinium photosensitizers such as methylene blue (MB) and toluidine blue (TB) produce singlet oxygen ($^1O_2$) and other reactive oxygen species (ROS) when exposed to red light in the presence of molecular oxygen (Gonzales et al. 2010; Rodrigues et al. 2012). Carotenoid-containing wild-type conidia of *N. crassa* are more tolerant than albino conidia to photodynamic treatments with methylene blue (Blanc et al. 1976).

Because the synthesis of carotenoids is induced by light in several fungi, these pigments might be expected to protect them against solar radiation (Zalokar 1955; Avalos et al. 1993, 2014; Libkind et al. 2004). The photoprotective role of carotenoids has been demonstrated in yeasts. Pigmented strains of *Sporobolomyces ruberrimus* and *Cystofilobasidium capitatum* were more tolerant to UV-B than the naturally occurring albino strains. In addition, the incremental increase in carotenoid contents during the stationary growth phase enhanced survivorship (Moliné et al. 2009). In the ascomycete *Neurospora crassa*, conidia from albino strains were less tolerant to UV-B than pigmented conidia of the wild type; this sensitivity was due to the lack of carotenoids, as indicated by the treatment of the wild type with the carotenogenesis inhibitor β-ionone during development of conidia (Morris and Subden 1974). Carotenoid-containing conidia of *N. crassa* were more tolerant than albino conidia to near-UV radiation (emission of the lamps ranged from 300 to 425 nm with maximum emission at 350 nm). However, the same strains were about equally sensitive to shortwave UV radiation (Blanc et al. 1976). Accumulation of carotenoids in conidia of *Neurospora* species seems to be an adaptive trait against solar UV radiation. *Neurospora* strains isolated from lower latitudes in Spain accumulated more carotenoids than strains isolated from higher latitudes. In addition, *N. crassa*, the species that accumulated high levels of carotenoids, was more tolerant to UV radiation than *N. discreta* or *N. tetrasperma* (Luque et al. 2012). A broader view of the biological roles of carotenoids in fungi is presented in another review in this special issue (Avalos and Limón 2015).

Non-chromogenic UV-absorbing compounds

Mycosporines were first detected in mycelia of different fungal species that demonstrated induction of sporulation by exposure to UV-B radiation (Leach 1965; Fayret et al. 1981). The two major functions attributed to mycosporines and mycosporine-like amino acids (MAAs) are their capacity to act as photoprotective UV filters or to regulate fungal sporulation (Bandaranayake 1998; Rezanka et al. 2004; Gao and Garcia-Pichel 2011; Nguyen et al. 2013; de Menezes et al. 2015). They may also have additional functions in fungi. For example, they may function as antioxidants, compatible solutes to protect cells against osmotic and thermal stress and desiccation, nitrogen reservoirs, and conidial germination inhibitors in different fungal species (Oren and Gunde-Cimerman 2007). First described in fungi, they are accumulated by a wide range of prokaryotic (cyanobacteria) and eukaryotic microorganisms (microalgae, yeasts, and filamentous fungi) (Sommaruga et al. 2004; Sinha et al. 2007; Libkind et al. 2011; Gao and Garcia-Pichel 2011). Mycosporines are widespread among the fungal classes Ascomycetes, Basidiomycetes, and the members of the old Zygomycetes (Leach 1965; Fayret et al. 1981; Bouillant et al. 1981; Bandaranayake 1998; Oren and Gunde-Cimerman 2007). They are also present in lichens (Nguyen et al. 2013) and in microcolonial fungi (Volkmann et al. 2003).

Mycosporines and mycosporine-like amino acids constitute a diverse family of low molecular weight

water-soluble, colorless, and UV radiation-absorbing secondary metabolites. They are composed of either an aminocyclohexenone or an aminocycloheximine ring, carrying nitrogen or imino alcohol substituents (Favre-Bonvin et al. 1976; Fayret et al. 1981; Bouillant et al. 1981; Bernillon et al. 1984). When substituted with amino acid residues, they are designated MAAs (Oren and Gunde-Cimerman 2007). Mycosporines present unique absorption spectra with a single, narrow, and strong absorption band that has a maximum between 310 and 365 and show no other absorption bands down to 210 nm (Gao and Garcia-Pichel 2011). The energy of the absorbed radiation is released in a short time through harmless thermal de-excitation without the production of ROS (Conde et al. 2004, 2007).

Mycosporines have been described as shikimate derivatives (Favre-Bonvin et al. 1987), but Balskus and Walsh demonstrated their biosynthetic origin from sedoheptulose-7-phosphate via the pentose phosphate pathway (Balskus and Walsh 2010; Nguyen et al. 2013). Mycosporines typically accumulate as solutes in the cytoplasm; but in some fungi, they can be excreted and thereby become important components of the mucilage that surrounds conidia (Young and Patterson 1982; Leite and Nicholson 1992; Gao and Garcia-Pichel 2011). Previous studies with plant-pathogenic fungi *C. graminicola* and *C. musae* showed that mucilage is chemically complex and contains UV-absorbing compounds such as mycosporines that absorb specifically at 240 and 310 nm (Leite and Nicholson 1992). It has been demonstrated that mucilage protects *Colletotrichum* conidia against the detrimental effect of UV radiation (Fernando et al. 2000; Mondal and Parbery 2005; de Menezes et al. 2015).

The synthesis and occurrence of mycosporines appeared to be linked to the sporulation process and they are considered biochemical markers for the reproductive states of fungi (Leach 1965; Fayret et al. 1981; Bandaranayake 1998; Gorbushina et al. 2003). Mycosporines are produced by sporulating mycelia or thallus of several fungal species, where they accumulate in spores and conidia (Leach 1965; Bouillant et al. 1981). The quantitative variation of mycosporines during thallus development and their accumulation inside the spores indicate translocation from sites of synthesis into reproductive cells (Bandaranayake 1998; Gorbushina et al. 2003).

In both yeasts and filamentous fungi, the mycosporine synthesis is stimulated by exposures to visible light and UV radiation, suggesting a photoprotective function (Leach 1965; Libkind et al. 2004). In addition to light intensity, their synthesis is highly dependent on the light source (Bandaranayake 1998). Near-UV radiation induces accumulation of mycosporines in mycelia of several fungal genera, but they are absent in non-sporulating colonies grown in the dark (Leach 1965; Bernillon et al. 1984).

As previously described with melanins and carotenoids, the accumulation of mycosporines in fungi appears to be an adaptive trait against solar UV radiation generated by natural selection. Mycosporine quantification and UV tolerance studies in Cystobasidiomycetes support the idea that the habitat of origin of each strain is important in the level of mycosporine synthesis, and that it has a photoprotective role in yeast (Libkind et al. 2011).

Information about the presence and importance of other non-chromogenic UV-absorbing metabolites to conidial tolerance to solar radiation is very limited. We isolated a novel UV-absorbing metabolite (named tyrosine betaine), which accumulates exclusively in *Metarhizium* conidia. It consists of betaine conjugated with tyrosine, and it was identified as 2-{[1-carboxy-2-(4-hydroxyphenyl)ethyl] amino}-*N*,*N*,*N*-trimethyl-2-oxoetanammoniun (chemical formula: $C_{14}H_{21}N_2O_4^+$; mass 281.1496, and maximum absorbance at 275 nm) (Carollo et al. 2010).

Antioxidants

Exposure to solar radiation can induce oxidative stress, and antioxidant defense systems are important in cellular protection against it (Jamieson 1998). Oxidative stress response in fungi involves both non-enzymatic and enzymatic defense systems (Rangel et al. 2015).

Non-ezymatic systems typically consist of small molecules, which are soluble in either an aqueous or, in some instances, a lipid environment (Jamieson 1998). They may include glutathione, mycosporins, mannitol, thioredoxins, carotenoids, and even melanins and melanin-like pigments, among others (Butler and Day 1998; Gonçalves and Pombeiro-Sponchiado 2005; Oren and Gunde-Cimerman 2007; Avalos and Limón 2015; Rangel et al. 2015). Mannitol is a well-known stress protector in several fungal species (Rangel et al. 2008, 2015). Conidia of *B. bassiana* knockout mutants of mannitol-1-phosphate dehydrogenase and mannitol dehydrogenase were less tolerant to UV-B radiation and H_2O_2-induced oxidative stress (Wang et al. 2012). Mannitol also induces the conversion of conidia to chlamydospore-like structures that confer enhanced tolerance to heat, drought, and UV-C radiation in *Gibberella zeae* (Son et al. 2012).

Cellular antioxidant defenses also include several enzymes that are capable of removing oxygen radicals and their products as well as repairing the damage caused by oxidative stress (Jamieson 1998). The enzymatic systems may include catalases, superoxide dismutases, glutathione reductases, glutathione peroxidases, glutathione-S-transferases, thioredoxin peroxidases, thioredoxin reductases, and methionine reductases, among others (Jamieson 1998; Huarte-Bonnet et al. 2015). We studied the activities of enzymes associated with oxidative stress

such as catalase-peroxidase, glutathione reductase, and superoxide dismutase in *M. acridum* and *M. robertsii* during conidial germination, mycelia growth, conidiation and in response to UV-B (from lamps), full-spectrum solar radiation, and solar UV-A. Conidia of the more UV-tolerant *M. acridum* strain ARSEF 324 displayed different isozyme profiles for all the enzymes when compared with the less tolerant *M. robertsii* strain ARSEF 2575. The levels of the three types of enzymes in both species were modulated during germination and by UV-induced stress (Miller et al. 2004). The inactivation of the genes *msrA* and *msrB* that encode methionine sulfoxide reductases in *A. nidulans* reduced conidial tolerance to UV radiation (Soriani et al. 2009). Conidia of *B. bassiana* knockout mutants for two manganese-cored superoxide dismutases were less tolerant to UV-A and UV-B radiation and to menadione or H_2O_2-induced oxidative stress (Xie et al. 2012). Catalases play different roles in the adaptation of *B. bassiana* to environmental stresses. The catalase family of *B. bassiana* consists of *catA* (conidia-specific), *catB* (secreted), *catP* (peroxisomal), *catC* (cytoplasmatic), and *catD* (secreted peroxidase/catalase) genes. Conidial tolerance to UV-B was reduced in all the disruption mutants except *catC*. UV-B tolerances of the knockout mutants *catA* and *catD* were reduced by 48 and 46 %, respectively (Wang et al. 2013). The antioxidant defense systems in entomopathogenic fungi are reviewed elsewhere in this special issue (Huarte-Bonnet et al. 2015).

DNA repair in conidia and germlings

CPDs and pyrimidine (6-4) photoproducts are the major DNA photoproducts induced by solar UV radiation. To counteract DNA damage, repair mechanisms specific for many types of lesions have evolved (Goldman and Kafer 2004; Ciccia and Elledge 2010; Verma and Idnurm 2013). NER and photoreactivation are the two major DNA repair systems responsible for repair of CPDs and 6-4PPs, but their relative importance varies considerably among different fungal species (Chelico et al. 2006). NER is a complex multi-step process involving the concerted action of approximately 30 proteins that replace dimers by de novo synthesis. Photoreactivation is a DNA repair mechanism performed by photolyases, which are light-dependent enzymes that monomerize dimers by using visible light as energy source. They absorb light in the blue spectrum and transfer an excited electron from the cofactor FAD to an enzyme-bound cyclobutane pyrimidine dimer, which is thereby cleaved (Sametz-Baron et al. 1997; Goldman and Kafer 2004; Bayram et al. 2008; Fang and St. Leger 2012; Kamileri et al. 2012; Kneuttinger et al. 2014). Photolyases show substrate specificity for either CPDs (CPDs photolyases) or 6-4PPs (6-4PP photolyases) (Kneuttinger et al. 2014).

As conidia of most fungal species are dormant or quiescent structures, sublethal damage to conidial DNA and to other cell biomolecules and structures caused by exposure to solar radiation is probably repaired only at the beginning of germination. The conditions in which conidia are maintained and germinated after UV exposure (i.e., temperature, lighting, culture media) strongly affect their recovery (Chelico et al. 2005, 2006; Chelico and Khachatourians 2008). A simple way of detecting photoreactivation is to compare the survival of conidia that remained in the dark after UV exposure to the survival of conidia that were exposed to photoreactivation wavelengths (375–425 nm) after UV exposure (Braga et al. 2002; Chelico et al. 2005). Photoreactivation is the principal mechanism for repairing UV-C-induced DNA damage in germlings of the entomopathogens *M. anisopliae* and *B. bassiana* (Chelico et al. 2006; Fang and St. Leger 2012). Fang and St. Leger (2012) used gene disruption to demonstrate that *M. robertsii* uses photolyases to remove UV-induced CPDs and 6-4PPs. Photoreactivation is also important for repairing UV-C-induced damage in germlings of the plant-pathogenic fungus *Fusarium oxysporium*. The *F. oxysporium* photolyase gene *phr1* is induced by visible light (Alejandre-Durán et al. 2003). The PHR1 photolyase plays a major role in photorepair in *Trichoderma atroviride* conidia, and a blue-light-UV-A photoreceptor is involved in *phr1* induction (Berrocal-Tito et al. 2007).

Cryptochromes are UV-A-blue-light receptors that have presumably evolved from the DNA photolyase–cryptochrome gene family. Bluhm and Dunkle (2008) identified two putative photolyase-encoding genes in the plant pathogen *Cercospora zeae-maydis*: *CPD1*, an ortholog of CPD photolyases described in other filamentous fungi, and *PHL1*, a cryptochrome/6-4 photolyase-like gene. After exposure to UV radiation, conidia with their *PHL1* gene disrupted had no photoreactivation capability and displayed reduced expression of *CPD1*, as well as *RAD2* and *RVB2*, which are orthologs of genes involved in NER and chromatin remodeling during DNA repair. This study provided evidence that *PHL1* regulates responses to UV irradiation (Bluhm and Dunkle 2008). In the genome of *A. nidulans* only one cryptochrome/photolyase-encoding gene, termed *cryA*, was identified. Protein CryA represses sexual development under UV-A (350–370 nm) and exhibits photorepair activity. This is another case in which one gene of this family displays sensory, regulatory, and repair activity (Bayram et al. 2008).

The 6-4 PP lesion found in DNA after UV irradiation is repaired by germinating conidia of *Neurospora crassa* (Baker et al. 1991). Chelico and Khachatourians (2008) isolated and characterized nucleotide excision repair-deficient mutants of *B. bassiana*. These mutants were also deficient in NER at their swollen-germinating conidial and blastospore life cycle stages.

Effects of solar radiation on conidia survival and germination

The deleterious effects of UV radiation on spores and conidia have been demonstrated in several taxonomic and ecology-based groups: e.g., entomopathogenic fungi such as *Metarhizium* (Zimmermann 1982; Morley-Davies et al. 1996; Fargues et al. 1996; Braga et al. 2001a, b, c, d, 2002; Yao et al. 2010; Nascimento et al. 2010), *Beauveria* (Morley-Davies et al. 1996; Fargues et al. 1996; Chelico et al. 2005, 2006; Fernandes et al. 2007; Chelico and Khachatourians 2008), *Paecilomyces* (Fargues et al. 1996; Chelico et al. 2006), *Simplicillium*, *Lecanicillium* (Braga et al. 2002; Chelico et al. 2006), and *Tolypocladium* (Santos et al. 2011); on plant-pathogenic fungi such as *Rigidoporus lignosus* (Liyanage et al. 1982), *Sclerotinia sclerotiorum* (Caesar and Pearson 1983), *Alternaria solani*, *Peronospora tabacina*, *Uromyces phaseoli* (Rotem et al. 1985), *Ustilago nuda* (Will et al. 1987), *Septoria tritici*, *S. nodorum* (Rasanayagam et al. 1995), *Uncinula necator* (Willocquet et al. 1996), *Mycosphaerella fijiensis* (Parnell et al. 1998), *Bremia lactucae* (Wu et al. 2000; Paul et al. 2012), *Phytophthora infestans* (Mizubuti et al. 2000), *Puccinia striiformis* (Cheng et al. 2014), and *Colletotrichum acutatum* (de Menezes et al. 2015); on litter fungi such as *Mucor hiemalis*, *Aspergillus fumigatus*, *Cladosporium cladosporioides*, *Leptosphaeria coniothyrium*, *Penicillium janczewakii, P. hordei*, *P. purpurogenum*, *P. spinulosum*, *Trichoderma viride*, *Ulocladium consortiale*, *Colonostachys rosea*, *Verticillium*, and *Marasmius androsaceus* (Moody et al. 1999), and on phylloplane fungi such as *Alternaria alternata*, *Botrytis cinerea*, *Epicoccum nigrum*, and *Ulocladium botrytis* (Moody et al. 1999; Costa et al. 2012). In fact, a few hours of exposure to UV-A and/or UV-B irradiance levels often found in nature, even in temperate regions, kill conidia of most fungal species (Braga et al. 2001d). In addition to killing the conidia, exposure to sublethal doses of UV radiation reduces conidial germination speed and consequently virulence, because virulence is related to germination speed of the conidia (Paul et al. 1997; Nascimento et al. 2010). The reduction in inoculum due to conidial photoinactivation and delay in germination is expected to reduce the propagation of diseases caused by pathogenic species and reduce the efficiency of entomopathogens used as bioinsecticides in situations with high UV irradiances. Of particular interest are situations in which conidia are exposed after field applications to UV irradiances and doses above those occurring in that fungal strain's original habitat, and therefore to which they are not adapted (Braga et al. 2002). The reduction in ozone layer and the consequent increase in UV-B irradiance, particularly at wavelengths between 290 and 315, may aggravate the problem (Caldwell and Flint 1997; Caldwell et al. 2007). We have demonstrated that an increase in UV-B irradiance drastically reduces the culturability of conidia of various species of the genus *Metarhizium* (Braga et al. 2001a, b, c) and that the negative effect of increased irradiance is higher during the growth phases in which the fungi are more susceptible to UV radiation, such as the late phase of conidial germination (Braga et al. 2001a). Molecular and physiological effects of solar UV radiation on conidia and conidia's functional responses are shown in Fig. 1.

DNA damage induced by UV radiation in conidia

The deleterious effects of UV radiation on conidial DNA have mainly been estimated indirectly, i.e., based on analysis of survival and on kinetics of germination (Braga et al. 2001a, b, c, d; Rangel et al. 2005a, b, c, 2011; Fernandes et al. 2007; Fuller et al. 2013; de Menezes et al. 2015). Few studies have quantified and/or characterized UV-induced damage in conidial DNA. Chelico et al. (2005) performed the first quantification of UV-C-induced CPD in *Beauveria bassiana* conidia. The maximum number of CPDs formed in DNA of *B. bassiana* conidia was 15 CPD 10 kb^{-1} after

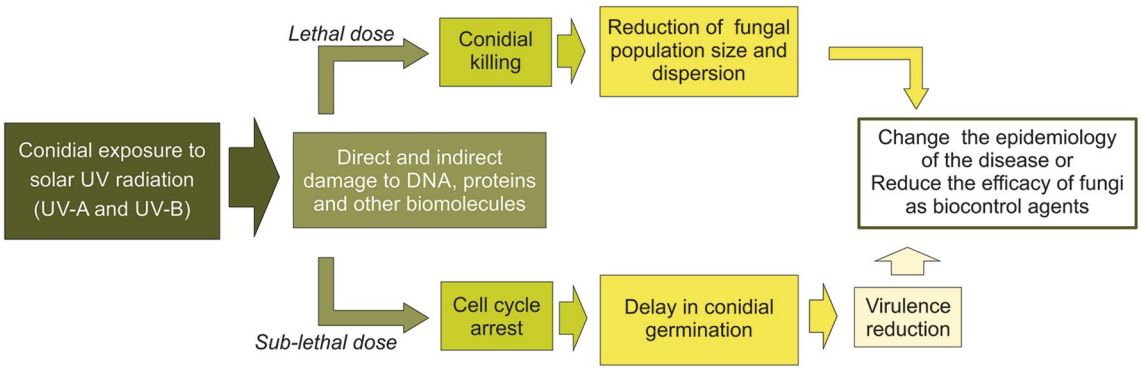

Fig. 1 Molecular and physiological effects of solar UV radiation on conidia and conidia's functional responses

a treatment with UV-C (peak intensity at 254 nm) and was quantified from conidia that were incubated to allow photoreactivation and nucleotide excision repair. This means the DNA was isolated after the UV-C-irradiated conidia were incubated in photoreactivating light for 6 h. The conidia incubated for photoreactivation and NER showed decreased number of CPD 10 kb^{-1} and a higher percent survival than conidia not allowed to repair after UV treatments (Chelico et al. 2005). Nascimento et al. (2010) estimated the effects of UV-B on ungerminated conidia of the fungi *A. fumigatus*, *A. nidulans*, *M. acridum*, and *M. robertsii* on the basis of CPDs quantification, surviving conidia analysis, and the evaluation of the germination kinetics of survival. CPDs were quantified in conidial DNA extracted immediately after UV-B exposures. A fluence-related induction of CPDs was observed in conidia of all the species. The frequencies of dimers were linear and directly proportional to the doses, but the CPD yields differed among species. The frequency of CPDs in *A. nidulans* conidia was similar to that in *M. acridum*, and both were lower than in *A. fumigatus*. According to the authors, the small size of *A. fumigatus* conidia (one-eighth of the volume of *A. nidulans*, and consequently having low cytoplasmatic absorption of UV radiation before reaching the nucleus) may be one of the factors responsible for the higher CPD frequency. The frequency of CPDs ranged from 0.04 (UV_{BE} dose of 0.9 kJ m^{-2} in *A. nidulans*) to 1.62 CPDs/10 kb (UV_{BE} dose of 5.4 kJ m^{-2} in *A. fumigatus*). It is important to point out that most of the UV_{BE} doses used in this study were sublethal to conidia of the fungi examined. Chelico et al. (2005) observed frequencies up to 28 CPDs 10 kb^{-1} in conidial DNA of *B. bassiana* after UV-C exposures (dose of 480 J m^{-2}). This unweighted UV-C dose killed approximately 100 % of the conidia.

It is well established that UV-B exposure delays the germination of surviving conidia (Rasanayagam et al. 1995; Nascimento et al. 2010; Costa et al. 2012). Nascimento et al. (2010) correlated the frequencies of UV-B-induced CPD in conidia with conidial germination kinetics. The delay in conidial germination was directly related to the CPD frequencies. The delay in conidial germination is probably a consequence of conidial cell cycle arrest in response to UV-damaged DNA. Several checkpoint mechanisms in fungi prevent cell cycle progressions until UV-damaged DNA has been repaired (Goldman et al. 2002; Nilssen et al. 2004; Dardalhon et al. 2008).

Unfortunately, all UV-induced damage studies with conidia previously cited used artificial light sources such as UV-C (Baker et al. 1991; Chelico et al. 2005, 2006; Chelico and Khachatourians 2008) or UV-B (Nascimento et al. 2010) lamps. These lamps have a spectral output composition very different from that of sunlight. Additionally, as far as we know, no attempt has been made to characterize or quantify photoproducts other than nuclear CPDs or 6-4PPs induced by UV radiation in conidial DNA. Thus, knowledge about conidial DNA photochemistry is still largely unknown, and additional studies are needed to identify and quantify other types of DNA lesions in nuclear and mitochondrial DNA. Conidia are very specialized cells with different structural, physiological, and biochemical characteristics compared to metabolically active cells. These differences may affect conidial DNA photochemistry. Other specialized structures involved in tolerance, such as bacterial spores, have marked differences in their DNA photochemistry compared to vegetative cells (Setlow 1995; Slieman and Nicholson 2000; Rebeil and Nicholson 2001; Moeller et al. 2009). The deleterious effect of UV-A radiation and visible light on conidia also needs to be better understood. Both UV-A and visible light at ecologically relevant intensities can inactivate conidia or spores of not only *Metarhizium* spp., but also other fungal species such as *S. lanosoniveum*, *L. aphanocladii* (Braga et al. 2001d, 2002), *Phytophtora ramorum* (Englander et al. 2006), and *Aspergillus niger* (Murdoch et al. 2013).

The deleterious effects of UV-B radiation are not restricted to DNA; proteins and lipids are also damaged (Trautinger et al. 1996). Heat shock proteins (mostly chaperones) are important in protein protection and repair and are differentially accumulated and/or are over-represented in conidial proteomes (Cooper et al. 2006; Noir et al. 2009; Barros et al. 2010; Oh et al. 2010). Quantitative and qualitative variations in conidial stored proteins can also affect stress tolerance and may explain, at least partially, differences between species (Cooper et al. 2006; Noir et al. 2009 Oh et al. 2010).

Variability in conidial tolerance to UV radiation

Tolerance to solar radiation varies widely among conidia of different species. In general, species with larger and pigmented conidia are more tolerant to solar radiation than species with smaller and hyaline conidia (Al-Rubeai and El-Hassi 1986; Ignoffo and Garcia 1992; Braga et al. 2001c; Chelico et al. 2006; Nascimento et al. 2010). Variability in tolerance to solar radiation also is great among isolates of the same species, and these variations can present continuous variation and a normal distribution at the populational level (Morley-Davies et al. 1996; Fargues et al. 1996; Braga et al. 2001a, b, c, d; Fernandes et al. 2007; Yao et al. 2010). This variability reflects the adaptation to different environmental conditions. Isolates from sites where the environmental levels of UV radiation are higher because of the lower latitude or the type of vegetation are more tolerant to UV-B radiation (Braga et al. 2001c; Bidochka et al. 2001; Singaravelan et al. 2008; Luque et al. 2012).

Unfortunately, little is known about the molecular mechanisms responsible for the great intraspecific variability in conidial tolerance to solar UV radiation. A comparison of isolates with contrasting tolerances would be interesting to determine the relative importance of different mechanisms responsible for UV tolerance. For example, do conidia of these isolates differ qualitatively and/or quantitatively to the already known UV protectants (such as sunscreens, HSPs, and antioxidants), in the efficacy of their DNA repair systems (such as NER and photoreactivation), or even in their morphology of the chromatin and the subcellular structures? Other interesting approaches would be proteomic and metabolomic analyses to identify stress-related proteins and metabolites differentially accumulated in conidia with contrasting tolerances to UV radiation.

Changes in UV tolerance during conidial germination

Not only ungerminated dormant conidia on sporulating colonies or during their dispersion, but also germlings, germ tubes, and appressoria at the time of infection can be exposed to solar UV radiation (Paul et al. 1997). In conidia of *M. acridum and M. robertsii*, UV tolerance varies during the different phases of germination. In relation to nongerminating conidia, there is a transitory increase in tolerance during the first germination hours (from 0 up to 4–6 h) followed by a pronounced decrease in tolerance as germination proceeded to germ tube emergence. The fact that all *Metarhizium* strains showed a transitory increase in UV tolerance during the first hours of germination indicates that conidial UV tolerance varies as a function of physiological state and cell cycle phase (see Braga et al. 2001a, b for a detailed discussion). It has been demonstrated for various species of filamentous fungi that duplication of DNA, which is a particularly sensitive period of the cell cycle to DNA damage, also occurs during the final phase of germination (Schmit and Brody 1976; Van Etten et al. 1983). In *Metarhizium*, the division of the nucleus is one of the last events of germination and only occurs after the formation of the germ tubes (St. Leger et al. 1989a, b).

Effects of the variation in environmental UV irradiance

Little is known about how variation in environmental UV irradiance affects fungal biology. This lack of information on the fungal response is not only limited to the effects on dormant conidia, but also concerns the effects of UV irradiance on the other stages of fungal life cycles. We have demonstrated that an increase in UV-B irradiance drastically reduces the culturability of conidia of various species of the genus *Metarhizium* (Braga et al. 2001a, b, c) and that the effect of increased irradiance is higher during the growth phases in which the fungi are more susceptible to UV radiation, such as the late phase of conidia germination (Braga et al. 2001a). Increase in UV-B irradiance reduces the germinability of *Puccinia striiformis* urediospores (Cheng et al. 2014) and influences the abundance and distribution of phylloplane fungi (Newsham et al. 1997).

Conidia and germlings at different germination stages of *M. acridum* were exposed to UV_{BE} from lamps at two irradiances, 920 or 1200 mW m^{-2}. By adjusting exposure time to provide the same dose, we found that there was no reciprocity in the lethal effects caused by UV_{BE} exposure. The higher irradiance exposure was always more damaging. Although non-reciprocity was observed in all situations, its magnitude varied as a function of metabolic state and/or cell cycle phase in which the germlings were at the exposure time. The least difference was observed when non-germinating conidia were exposed, and the highest was observed when conidia were exposed during an advanced germination phase (after germ tube emergence). Because most evaluations of UV tolerance in filamentous fungi used only non-germinating conidia, it is clear that the effects of irradiance on the complete life cycle of the fungi tend to be underestimated. Our findings illustrate that the intensity of irradiation, as well as the dose, is important. The data are consistent, however, with the fungus displaying some degree of protection and repair against near-UV damage when the dose is administered slowly or at low doses, but protection and repair become overwhelmed as irradiation dose increases above a threshold (Braga et al. 2001c). Fargues et al. (1997) observed lower reciprocity with exposures to UV-B >280 nm than with exposure to UV-B >295 nm to germination and viability of the insect-pathogenic fungus *Paecilomyces fumosoroseus*. In the first case, the effects of the higher irradiance were more pronounced. Owens and Krizek (1980) reported that at low irradiance, UV radiation (265 nm) was less effective in preventing germ tube emergence than at high irradiance in the phytopathogenic fungus *Cladosporium cucumerinum*. The study also showed that, in contrast to what was observed for the 265 nm radiation, reciprocity was almost complete when a radiation of 325 nm was used.

Field experiments

We performed field experiments to determine the effects of exposures to full-spectrum sunlight and solar UV-A radiation on conidial survival and germination of *M. acridum* and *M. robertsii* strains (Braga et al. 2001d). Exposures were performed during the summer (Logan, UT, USA,

41.5°N latitude, 1.5 km elevation). The strains showed wide variation in tolerances when exposed to full-spectrum sunlight as well to as to UV-A sunlight. 4-h exposures to full-spectrum sunlight reduced relative survival by approximately 30 % for *M. acridum* strain ARSEF 324 and by 100 % for *M. robertsii* strains ARSEF 23 and 2575. The relative UV sensitivity of the two more sensitive strains was different under natural solar UV compared with artificial UV-B radiation at 290–320 nm in the laboratory. Strain ARSEF 2575 was more tolerant than strain ARSEF 23 to artificial UV-B radiation, but less tolerant to solar UV radiation. This happened because strain ARSEF 2575 is less tolerant than strain ARSEF 23 to UV-A which is the major component of solar UV radiation (Braga et al. 2001a, b, c). 4-h exposures to solar UV-A reduced the relative survival by approximately 10 % for strain ARSEF 324, 40 % for strain ARSEF 23, and 60 % for strain ARSEF 2575 (Braga et al. 2001d). These data emphasize the importance of using a realistic UV spectrum in UV experiments with insect-pathogenic fungi. Exposures to both full-spectrum sunlight and UV-A sunlight delayed the germination of the surviving conidia of all three strains. In addition to confirming the deleterious effects of UV-B, the results clearly demonstrate the negative effects of UV-A sunlight on the survival and germination of *M. anisopliae* conidia under natural conditions. The negative effects of UV-A sunlight also emphasized that the biological spectral weighting functions for this fungus must not neglect the UV-A wavelengths (Braga et al. 2001d).

Direct exposure to solar radiation also reduced the viability of the different types of spores of several ascomycete, basidiomycete, and oomycete fungi such as *Rigidoporus lignosus* (Liyanage et al. 1982), *Sclerotinia sclerotiorum* (Caesar and Pearson 1983), *Peronospora tabacina*, *Uromyces phaseoli*, *Alternaria solani* (Rotem et al. 1985), *Phytophthora infestans* (Mizubuti et al. 2000), *Bremia lactucae* (Wu et al. 2000), and *Venturia inaequalis* (Aylor and Sanogo 1997) among several other species (Ulevičius et al. 2004).

Improving conidial tolerance to UV radiation in entomopathogenic fungi

Several attempts have been made to reduce the negative effects of UV radiation on conidia of entomopathogenic fungi by (a) selecting strains more tolerant to radiation (Morley-Davies et al. 1996; Fargues et al. 1996; Braga et al. 2001c; Yao et al. 2010), (b) manipulating the fungal growth conditions (i.e., light conditions, culture media) (Rangel et al. 2005a, b, 2006a, b, 2008, 2011, 2015), (c) genetic engineering of the strains (Tseng et al. 2011, 2014; Shang et al. 2012; Fang and St. Leger 2012; Wang and Feng 2014), and (d) adding photoprotective agents to the conidial formulations (Moore et al. 1993; Alves et al. 1998; Hedimbi et al. 2008).

Expression of a highly efficient CPD photolyase from the Archaea *Halobacterium salinarum* increased photorepair >30-fold in both *M. robertsii* and *B. bassiana* and the transgenic strains were much more tolerant to sunlight (Fang and St. Leger 2012). Genetic engineering of the entomopathogenic fungus *B. bassiana* to overexpress an exogenous tyrosinase gene from *A. fumigatus* improved fungal production of melanin and thereby increased both the UV tolerance and virulence of conidia (Shang et al. 2012). Similarly, the transformation of *M. anisopliae* to express the polyketide synthase (PKS), 1,3,4-trihydroxynaphthalene reductase (Thr) and scytalone dehydratase (Scd) genes from *Alternaria alternate* enabled the fungus to produce melanin. The transformant strain, which is capable of expressing exogenous DHN melanin, exhibited an increased tolerance to UV radiation, high temperature, and desiccation (Tseng et al. 2011, 2014).

The isolation of intrinsically tolerant strains and the manipulation of the physical and nutritional environments are two interesting approaches to obtain conidia more tolerant to stresses, because they do not involve genetic modifications of the strains. Government approval for genetically engineered strains as bioinsecticides is currently difficult to obtain, particularly in Europe. Elevated tolerance to UV radiation and heat is acquired in *Metarhizium* conidia when the fungus is exposed during mycelial growth to other sublethal stresses. This is due to a cross-protection phenomenon that occurs because the response against the different stress-generating factors shares several of their components (Liu et al. 2013; Ortiz-Urquiza and Keyhani 2015). Conidia of *M. robertsii* produced under nutritive stress and osmotic stress have elevated tolerance to UV-B radiation (Rangel et al. 2008, 2015). With *M. acridum* strain ARSEF 324, strong selective pressure for tolerance to stress in its natural environment reduced the phenotypic plasticity in UV-B tolerance; but did not affect the phenotypic plasticity of other traits such as conidial morphology and germination speed (Rangel et al. 2005b).

We described the protective role of visible light to subsequent UV-B exposure in *M. robertsii* (Rangel et al. 2011). *M. robertsii* grown under moderate visible light intensity (5.4 W m^{-2}) produced conidia that were at least twice as tolerant to UV-B radiation as conidia produced in the dark (Rangel et al. 2011). This is the same protective effect described in *A. fumigatus* (Fuller et al. 2013) and *C. acutatum* (de Menezes et al. 2015). In *A. fumigatus*, exposure of dark-grown fungus to blue light increased tolerance to subsequent exposure to either UV or hydrogen peroxide, relative to colonies kept in the dark prior to exposure (Fuller et al. 2013). In *C. acutatum*, colonies exposed to

light produced approximately 1.7 times more conidia than colonies grown in continuous darkness. The UV-B tolerances of conidia produced under light were at least two times higher than those of conidia produced in the dark (de Menezes et al. 2015). The ability of visible light to increase UV tolerance was also demonstrated in *C. neoformans* (Verma and Idnurm 2013).

Conclusions

Solar UV radiation is highly detrimental to conidia and is one of the major environmental factors responsible for controlling natural fungal populations. Conidia are killed both by UV-A and UV-B. In additional to killing conidia, sublethal exposures to solar radiation slow germination speed and reduce the virulence of pathogenic species. Conidial tolerance to solar radiation is a polygenic and quantitative trait which involves several protective mechanisms that prevent or reduce the occurrence of damage to cellular components (i.e., sunscreen pigments, antioxidants, molecular stabilizers), as well as several systems that repair UV-induced damage during conidial recovery (i.e., NER, photoreactivation, chaperones). The action of these mechanisms sometimes overlaps.

Despite the increasing understanding of some of these systems, both with conidia and germlings, many of them are only superficially comprehended. The discovery of new molecules and/or mechanisms involved in conidial tolerance to solar radiation will contribute to a better understanding of the persistence, dispersal, and germination of pathogenic species in the environment, and to the development of entomopathogenic fungal strains with increased stress tolerance for use in the biocontrol of insect pests.

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