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Review

How light affects the life of *Botrytis*

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ABSTRACT

Fungi, like other organisms, actively sense the environmental light conditions in order to drive adaptive responses, including protective mechanisms against the light-associated stresses, and to regulate development. Ecological niches are characterized by different light regimes, for instance light is absent underground, and light spectra from the sunlight are changed underwater or under the canopy of foliage due to the absorption of distinct wavelengths by bacterial, algal and plant pigments. Considering the fact that fungi have evolved to adapt to their habitats, the complexities of their 'visual' systems may vary significantly. Fungi that are pathogenic on plants experience a special light regime because the host always seeks the optimum light conditions for photosynthesis – and the pathogen has to cope with this environment. When the pathogen lives under the canopy and is indirectly exposed to sunlight, it is confronted with an altered light spectrum enriched for green and far-red light. *Botrytis cinerea*, the gray mold fungus, is an aggressive plant pathogen mainly infecting the above-ground parts of the plant. As outlined in this review, the Leotiomycete maintains a highly sophisticated light signaling machinery, integrating (near)-UV, blue, green, red and far-red light signals by use of at least eleven potential photoreceptors to trigger a variety of responses, i.e. protection (pigmentation, enzymatic systems), morphogenesis (conidiation, apothecial development), entrainment of a circadian clock, and positive and negative tropism of multicellular (conidiophores, apothecia) and unicellular structures (conidial germ tubes). In that sense, 'looking through the eyes' of this plant pathogen will expand our knowledge of fungal photobiology.

1. Introduction

Light is an important environmental factor in almost all ecosystems by being a source of energy, information as well as stress. While several organisms use light for energy generation (photosynthesis), all organisms have to protect themselves against the harmful effects of light such as the damage inflicted on macromolecules by the UV fraction and by emerging singlet oxygen and other reactive oxygen species (ROS). Light may be also associated with elevated temperatures, leading to desiccation and osmotic stress. Finally, organisms may use light, or its absence, to interpret their surroundings and adapt to environmental changes for ensuring survival and to schedule reproduction.

In contrast to budding yeasts, which can only respond to light indirectly, filamentous fungi maintain a complex regulatory network of light-sensitive proteins (photoreceptors) and signal transduction pathways that allows them to use light (quantity, direction, quality) as a signal to induce adaptive responses (protection, e.g. by enzymatic systems and secondary metabolites), to control development (tropism, morphogenesis) and to run a circadian clock (entrainment/resetting) (Herrera-Estrella and Horwitz, 2007; Rodriguez-Romero et al., 2010). Well-studied models in fungal photobiology are the saprophytes *Neurospora crassa* and *Aspergillus nidulans*, which belong to the classes of the Sordariomycetes and the Eurotiomycetes of the Ascomycota, respectively. Light regulates carotenogenesis, conidiation, protoperithecia formation and the circadian clock in *N. crassa* (Linden et al., 1997), and secondary metabolism and the balance between sexual (cleistothecia formation) and asexual development (conidiation) in *A. nidulans* (Bayram et al., 2010). Excellent reviews describe the progress in understanding photobiology in these two models and few other species (Avalos and Estrada, 2010; Chen et al., 2010b; Corrochano and Garre, 2010; Idnurm et al., 2010; Schmoll et al., 2010; Carreras-Villaseñor et al., 2012; Dasgupta et al., 2016; Fischer et al., 2016; Fuller et al., 2016).

However, little is known about the role of light in plant pathogens. In these fungi, the property to sense and to react to light may be important to become successful pathogens by affecting the infection process (interaction with the host) and/or their overall fitness (success in dispersal, survival or achieving genetic diversity *via* sexual recombination). Notably, plant pathogenic fungi, especially those infecting the aerial plant organs, are faced with an exceptional light regime due to depletion of red and blue light that is absorbed by the plant for photosynthesis and the surplus of green and far-red light that is reflected and/or transmitted by the plant tissue. Plants likewise sense the light environment in order to optimize the conditions for

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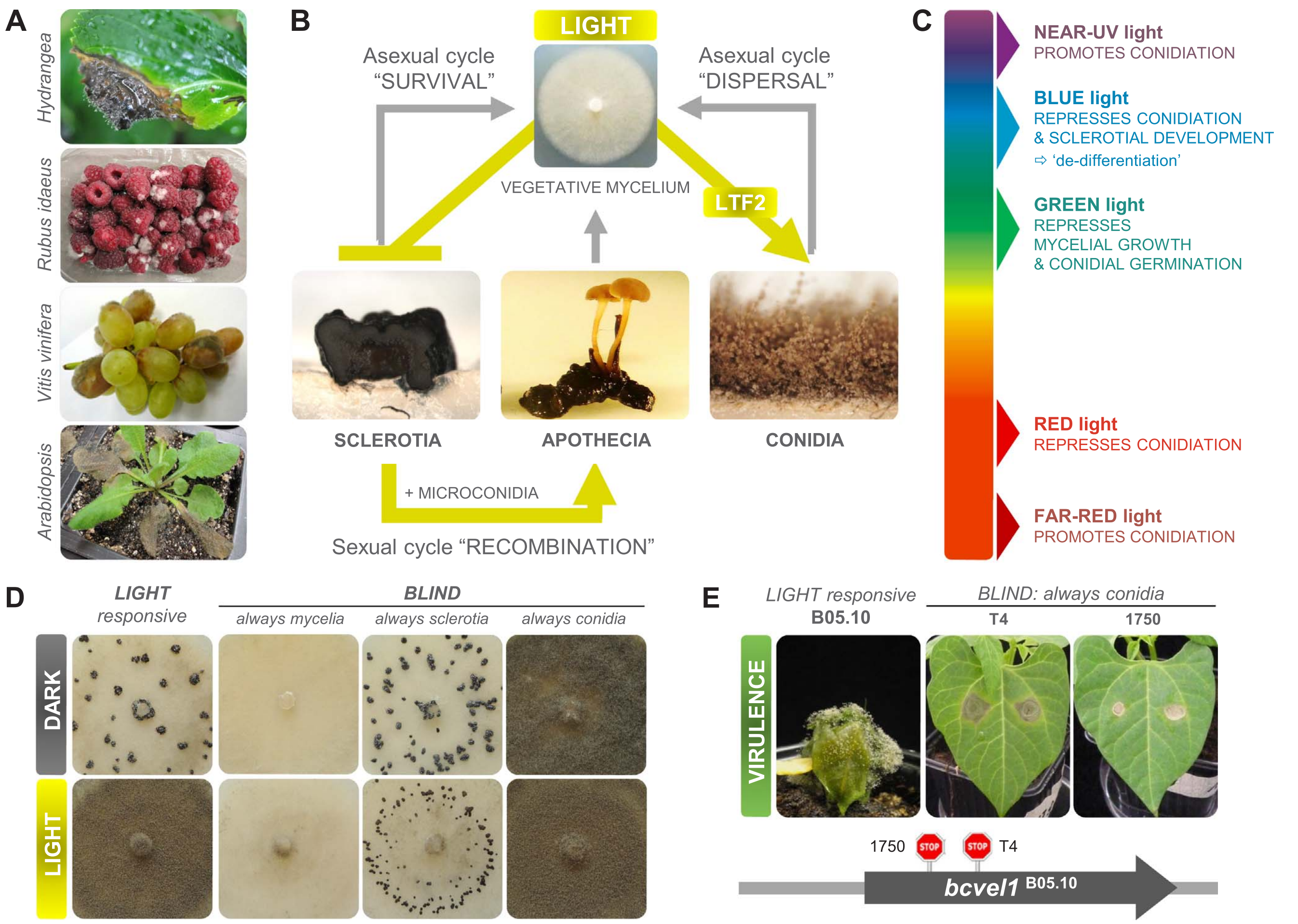

Fig. 1. Photomorphogenesis in *B. cinerea*. (A) *B. cinerea* causes gray mold diseases in many plant species. *A. thaliana* can be infected in the laboratory, but is likely not a 'natural' host of *B. cinerea* due to its high basal resistance. (B) Reproduction cycles of *B. cinerea* B05.10. Vegetative mycelia differentiate conidiophores and conidia when incubated in the light and sclerotia in constant darkness. The sclerotia may germinate with mycelia and conidiophores, or with fruiting bodies (apothecia) after fertilization with microconidia of the opposite mating type has taken place. Apothecia are only differentiated in the light. (C) Five light qualities affect the growth behavior of *B. cinerea*. Full-spectrum light induces the formation of conidia which is accompanied by the repression of sclerotial development, while monochromatic light has positive or negative effects on conidiation (Tan, 1975). Green light impairs mycelial growth and conidial germination but has no effect on the differentiation of the reproduction structures (Zhu et al., 2013). (D) Not all *B. cinerea* strains undergo photomorphogenesis. Three different *blind* phenotypes are observed; the mode of reproduction is no longer determined by light in comparison to *light-responsive* strains such as B05.10. Top views of two-week-old cultures are shown. (E) The *always conidia* phenotype may be associated with reduced virulence. Loss-of-function mutations in the Velvet protein BcVEL1 are the reason for the phenotype in the wild isolates T4 and 1750 (Schumacher et al., 2013, 2012).

photosynthesis and growth. Therefore, a low red:far-red ratio indicates the presence of competitors (shading by other plants) and triggers the shadow avoidance response. UV and blue light are indicative of gaps in the canopy, and consequently counteract this response (Fraser et al., 2016). Taken together, leaf pathogens have to cope with the high-light conditions the hosts aspire to. In addition, plant pathogens in the temperate climate zones need to survive several months each year without a living host.

A plant pathogen of high relevance and with a striking life cycle is *Botrytis cinerea*, the causal agent of gray mold diseases in more than 500 plant species (Elad et al., 2016) (Fig. 1A). It belongs to the class Leotiomycetes, and can be considered as the best studied species of the genus *Botrytis* that comprises 34 recognized species to date. *Botrytis* ssp. are primarily necrotrophs which kill the host cells before decomposing the plant tissue for promoting their own growth and reproduction (van Kan, 2006; Williamson et al., 2007). Recent studies have also described systemic and symptomless infections by *Botrytis* spp., indicating that the fungus may also behave like an endophyte (van Kan et al., 2014; Shaw et al., 2016). In viticulture, *B. cinerea* plays an ambivalent role as it may cause bunch rot, the common detrimental infection, or in rare cases noble rot, a beneficial infection enabling the production of sweet botrytized wines (Maygar, 2011). As *B. cinerea* prefers high humidity and moderate temperatures (no/poor growth above 30 °C), its occurrence in the field is restricted to the temperate climate zones. However, as a postharvest pathogen on fruits, vegetables and flowers in cold storage, *B. cinerea* is a worldwide threat. A more detailed description of the pathogen and its management in agricultural systems can be found elsewhere (Fillinger and Elad, 2016). The life cycle of *B. cinerea* includes vegetative mycelia, (macro-)conidia for dispersal, sclerotia for survival and the latter structures also as the pre-requisite for sexual development (female mating partner), microconidia as male gametes, and fruiting bodies (apothecia) with ascospores as sexual structures (Fig. 1B). The formation of high numbers of conidia is typical for the summer season when the chances of reaching a living host are high. On the other hand, sclerotia allow for enduring the winter season and germinate asexually or sexually (by bearing apothecia) in the following spring (Williamson et al., 2007).

The influence of light on the morphology and the growth behavior of this fungus has been realized more than a hundred years ago, but different experimental conditions and the high levels of phenotypic diversity between different *B. cinerea* strains led to several conflicting observations (Klein, 1885; Peltier, 1912; Robinson, 1914; Brierley, 1921; Godfrey, 1923; Paul, 1929; Barnes, 1930). More detailed studies on light effects in the 1970's have demonstrated that *B. cinerea* exhibits