REVIEW

Key role of environmental competence in successful use of entomopathogenic fungi in microbial pest control

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Abstract
One of the main negative effects of climate change on biological pest control is alteration of relationships between insect pests and their natural enemies (both entomophagous and entomopathogenic). Indeed, environmental conditions can have multiple effects on pest control success when using entomopathogenic fungi (EPF), where conidial depletion, inactivation, and loss in virulence and infectivity can all occur. Appropriate mass production and formulation strategies for EPF can partially solve these problems. However, the only strategy to guarantee high virulence and infectivity is selection of environmentally competent fungal strains that are able to persist in the host environment for the required infection period. This review examines the criteria for selection of environmentally competent EPF. While UV radiation, followed by humidity and temperature, is probably the most important propagule depletion and inactivation factors in epigeal habitats, temperature is most critical for reducing the infectivity and virulence of EPF in epigeal and hypogeal habitats. In addition, geographical origin and other biotic and abiotic factors have an important impact which may guarantee the environmental competence of selected entomopathogenic fungal strains and, therefore, farmer willingness to replace chemicals with mycoinsecticides. To achieve this, it is urgent to promote the development of microbial control solutions adapted to relatively uniform climatic zones through more simplified, targeted, and less costly EPF approval and authorization.

Key message

- Climate change alters relationships between arthropod pests and entomopathogenic microorganisms.
- Success of EPF in microbial pest control is highly affected by the environmental competence of the selected fungal strains.
- Temperature is a key climatic factor limiting entomopathogenic fungal virulence in both epigeal and hypogeal habitats.
- UV radiation is a critical abiotic factor causing EPF conidial depletion and inactivation in epigeal habitats.
- Biocontrol solutions based on EPF should be based on the use of environmentally competent fungal strains adapted to relatively uniform climatic zones.

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Introduction

Modern agriculture is confronted with two critical challenges: the mitigation and adaptation to climate change. Addressing these challenges has compelled authorities and farmers to find ways to ensure food security and safety through agricultural sustainability and integrated pest management (Hillocks 2012). Arthropod pests, particularly insects that are responsible for 10–16% of global crop production losses each year, have significantly increased in agricultural and forestry areas as a result of anthropogenic perturbations (e.g., climatic change and globalization) (Savary et al. 2019). These ecosystem impacts have encouraged the spread of insect pests including invasive species that are now reaching areas where they have never been present before (Skendžić et al. 2021).

Although the consequences of climate change on pest incidence and their control are not fully understood, some evidence suggests that pest distribution range, insecticide usage, and the relationship between insect pests and their natural enemies could be influenced by climate change (Skendžić et al. 2021). Generally speaking, the expected secondary effects of climate change on agricultural insect pests are: an increased number of generations per year; greater overwintering survival; expansion of their natural geographical range; and desynchronization of insects, their natural enemies, and host plants (Bale et al. 2002; Quesada-Moraga 2011; Bebber et al. 2013; Skendžic, et al. 2021). In the same vein, climate change can also affect insecticide usage and residue persistence; while the expanded distribution of insect pests could promote the use of a greater variety of insecticides at increased rates and frequencies, it could also increase the likelihood of insecticide resistance development (Delcour et al. 2015). Furthermore, climate change could also facilitate insecticide dissipation due to increased volatility and faster degradation, both of which are increased by high relative humidity, high temperatures, and increased exposure to sunlight (Delcour et al. 2015). There is also evidence of a potential effect of climate change on the relationship between insect pests and their natural enemies, both entomophagous (predators, parasitoids) and entomopathogenic (microbes). Regarding the former, a negative impact of climate change on natural predation and parasitism has been demonstrated due to life cycle time lags between prey and predators, or between hosts and parasitoids (Stireman et al. 2005; Thomson et al. 2010; Skendžic et al. 2021). Regarding the latter, restrictive environmental conditions, particularly temperature, humidity, and UV-B radiation, could severely limit the success of microbial control.

Microbial control of insect pests is considered to be one of the most viable alternatives to synthetic chemical insecticides (Eilenberg 2006). The current importance of inoculative and inundative microbial pest control strategies in an adapting crop protection world scenario and the sustainability requirements for agriculture have created major scientific and technical challenges. At this respect, the identification and selection of the most virulent and environmentally competent microbial control agents are essential to develop effective strategies that can be used within integrated pest management programs (Jackson and O'Callaghan 1997; Jackson et al. 2000).

The environmental competence of microbial control agents, specifically microbes, relies on the ability of an applied microbe to persist and even multiply within the pest's environment (Jackson and O'Callaghan 1997; Jackson et al. 2000). While obtaining the desired level of control of the target pests is a key factor to select successful microbial control agents, their environmental competence should also be considered a critical factor (Jackson and O'Callaghan 1997; Jackson et al. 2000). Particularly, the success of entomopathogenic fungi (EPF) in pest biocontrol is highly dependent on their persistence in the host's environment for the required infection period, which suggests that environmental competence is not only a desirable factor, but also a key consideration for the success of EPF within integrated pest management plans (Jackson and O'Callaghan 1997; Jackson et al. 2000).

We hereby examine the criteria for the selection of environmentally competent EPF, addressing key questions about the ecological requirements and the possible influence on the target pest based on this environmental competence particularly geographical origin and habitat of isolation of fungal strains. This ecological knowledge is crucial for the development of accurate predictive models and the use of selected fungal control agents under appropriate conditions when they are introduced into an ecosystem. Overall, the selection of environmentally competent fungal strains is the best option to guarantee the desired level of control and, hence, to promote the acceptance of farmers and willingness to progressively replace chemical insecticides using EPF as microbial control agents.

Entomopathogenic fungi and environmental competence

Entomopathogenic fungi, with particular focus on hypocrealean ascomycetes, are unique among entomopathogenic microorganisms due to their mode of action through the cuticle which gives them a significant advantage in integrated pest management strategies; conidia of EPF adhere to the cuticle, germinate, penetrate the host (without the need for ingestion), grow inside the hemocoel, and finally cause the death of the host due to nutrient depletion and invasion

of internal tissues and organs, and/or the secretion of proteins and/or secondary metabolites with insecticidal effects (Vega et al. 2012). After host death hyphae emerge from the cadaver and produce conidiophores and conidia, enabling the fungus to infect new hosts through horizontal transmission (Vega et al. 2012). Today there are numerous and ever-increasing numbers of biopesticides available on the market, mainly based on hypocrealean ascomycetes, such as species in the genera *Beauveria* Vuill., *Metarhizium* Sorokīn, *Akanthomyces* Lebert, and *Cordyceps* Fr.. (Ascomycota: Hypocreales). These fungi are able to control a wide range of arthropod pest species, including locusts and grasshoppers, soil dwelling insects, piercing and sucking insects, mites, stored-grain pests, several forestry pests, as well as invasive, medical and veterinary pests (Quesada-Moraga et al. 2020).

Together with improving the killing speed of these fungi, one of the greatest challenges for improving the efficacy of EPF as mycoinsecticides is to develop new ways to overcome the negative effects of solar radiation, low humidity, and excessive temperature requirements (Jackson et al. 2010; Jaronski 2010). These abiotic factors significantly affect both the likelihood of successful and rapid initial infection by EPF, and their ability to persist in the target host's environment, at least for the time needed to ensure subsequent infections and to enhance the probability of secondary transmission and epizootics developing (Braga et al. 2001a, b). Hence, pest control strategies that include EPF require a biorational approach for selection of strains based on, not only their intrinsic virulence against the target host and the limited impact on nontargeted arthropods, but also on their efficacy over the range of environmental conditions they are likely to encounter post application. Various studies have demonstrated the high efficiency of EPF for control of particular insect or mite pests under laboratory conditions. However, even in cases where fungi show consistently good results in large-scale trials in particular regions, their lack of environmental competence under more extreme environmental conditions that affect infection and persistence partly explains their inconsistent results in other regions; this decreases the popularity of mycoinsecticides compared with synthetic chemicals insecticides (Acheampong et al. 2020; Alali et al. 2019; González-Mas et al. 2019; Han et al. 2021; Jaronski 2010; Maina et al. 2018; Paixão et al. 2019; Shang et al. 2012; Vänninen 1999; Wu et al. 2020).

The capability of EPF varies under diverse abiotic environmental scenarios at the strain (below-species) level; thus, the best strategy to increase their use is to determine the tolerance of individual strains to specific environmental constrains and to match these to the environment in which they will be used based on their tolerance to the major climatic stresses (Couceiro et al. 2021; Fernández-Bravo et al. 2016, 2017; Quesada-Moraga and Santiago-Álvarez 2008). When considering a lack of environmental competence in a given fungal strain, it is important to distinguish whether this is because (1) the infective propagule is killed or inactivated or (2) infectivity or virulence had been reduced due to suboptimal climatic conditions. While formulation techniques can partially protect propagules from environmental inactivation, either in epigeal or hypogeal habitats, the strategy to increase the high virulence potential of EPF is the selection of environmentally competent fungal strains, which could even reduce the use of protectants (Jackson and O'Callaghan 1997; Jackson et al. 2000; Jaronski 2010). In this respect, it is crucial to identify the most important abiotic climatic factors that affect propagule inactivation and virulence (Fig. 1). Previous work has shown that temperature has a critical role in environmental competence and entomopathogenic fungal strain virulence, while the roles of sunlight and humidity on virulence are less clear (Fig. 1) (Acheampong et al. 2020; Fernandez-Bravo et al. 2017; García-Fernández et al. 2008; Quesada-Moraga et al. 2006; Vidal et al. 2003).

Temperature

Temperature is a key factor driving efficacy of EPF in microbial pest control, with thermal stress influencing their entire infection pathway (Paixão et al. 2019). In general, EPF are mesophilic microorganisms with growth potential between 10 and 40 ºC and optimal growth ranging from 25 to 35 ºC, and the geographical origin of an entomopathogenic fungal strain is a key factor determining tolerance to high or low temperature (López-Plantey et al. 2019; Membang et al. 2021; Onsongo et al. 2019; Paixão et al. 2019; Quesada-Moraga and Santiago-Álvarez 2008; Seid et al. 2019). Some fungal proteins are activated by temperature; differences in proteins have been observed in cold active strains grown at 8 °C compared with 25 °C, but such differences were not observed in a non-cold active strain (De Croos et al. 2001). These differentially expressed proteins could influence fungal virulence. It is possible that some strains have genes related to thermotolerance which could have an effect on strain virulence (Zhang et al. 2011).

High and low temperatures are known to be major limiting factors for growth of EPF such as *Beauveria* and *Metarhizium* (Mann and Davis 2020; Muniz et al. 2020). Phenotypic and molecular insights into heat tolerance of EPF have been reviewed recently (Tong and Feng 2020), providing wide evidence for the high sensitivity of *Beauveria* and *Metarhizium* to high temperatures beyond their upper thermal limits (32–35 °C) during summer months. Under Mediterranean climate conditions, heat tolerance is a critical factor limiting the efficacy of mycoinsecticide field applications (Tong and Feng 2020). Apart from the strain origin, the inoculum production technologies could help achieve more heat-tolerant conidia. The use of genetic engineering of candidate

Fig. 1 Impact of abiotic climatic factors on mortality and virulence of the infective propagules of entomopathogenic fungi. Solid connecting arrows represent direct effects while stippled connecting arrows represent solutions to minimize the impact
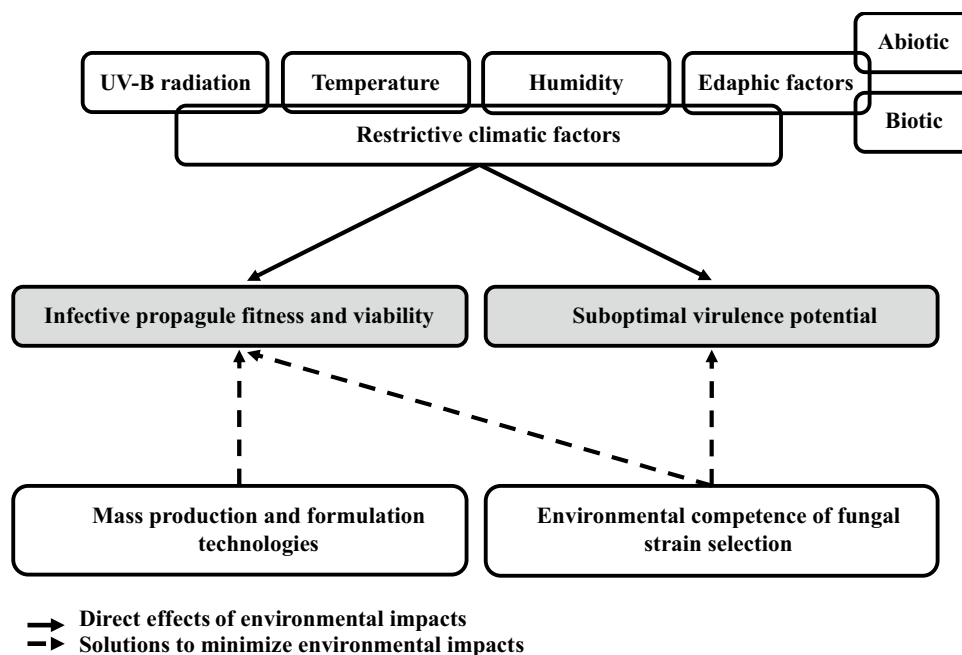
strains for enhanced heat tolerance could be a tool to increase knowledge on the molecular basis of fungal heat tolerance and its multiple regulatory pathways (Tong and Feng 2020). Also, selection of propagule for production and application could be important as temperature optima can vary even in the same strain; in *Metarhizium brunneum* Petch (Ascomycota: Hypocreales) strain EAMa 01/58-Su, the most suitable temperature for conidial production (26.3 °C) differs from the temperature for microsclerotia germination (22.7 °C) (García-Fernández et al. 2008; Yousef-Yousef et al. 2022). The correct choice of the propagule may be decisive for a successful integrated pest management strategy.

The role of temperature in determining the environmental competence of entomopathogenic fungal strains has been illustrated in greenhouse trials of whitefly [*Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrodidae)] control in tomato grown in Seville, Spain (Santiago-Álvarez et al. 2002); a non-commercial formulation of a *Beauveria bassiana* (Bals.-Criv.) Vuill. (Ascomycota: Hypocreales) strain from local soil was 90% efficient, not significantly different from a neonicotinoid-based conventional treatment, and twice as efficient as a commercial mycoinsecticide (Santiago-Álvarez et al. 2002). Since the temperature averaged 26 °C and peaked at 43 °C during the experiment, it was unsurprising that the local strain used (25.1 °C optimum and 36 °C maximum temperature) was an effective biocontrol agent because it could be active over a much longer time each day than the commercial strain (20 °C optimum and 32 °C maximum temperatures) (Fig. 2).

To date, the development of new mycoinsecticides is time-consuming and costly. In addition, there is a global trend for the use of registered fungal strains worldwide, with very little chance of them being successful in all regions due to lack of environmental competence. This encourages farmers to believe that mycoinsecticides are unable to protect their crops. To this end, there are available tools using temperature-dependent models to predict spatially suitable geographical areas for deployment of fungal strains as a function of their thermal biology (Agbessenou et al. 2021; Kamga et al. 2022). Use of entomopathogenic fungal strains for pest control in agroforestry systems, where they are not environmentally competent, shows a complete lack of scientific, economic, and environmental sense.

Sunlight

Sunlight, particularly the UV-B component, is probably the most important factor contributing to inactivation of fungal propagules on exposed surfaces such as the phylloplane of plants. The use of UV light protectants in conidial formulations was the first strategy used to counter the effects of UV-B, but in many cases, this strategy had a limited effect (Jaronski 2010).

Mass production and formulation strategies can also influence UV-B tolerance in several fungal biocontrol agents. For example, EPF have a higher stress tolerance when produced under white light than when they are produced in darkness (Dias et al. 2021). Various outcomes on conidial stress tolerance and gene expression have been reported in *Metarhizium robertsii* J.F. Bisch., S.A. Rehner & Humber (Ascomycota: Hypocreales) during
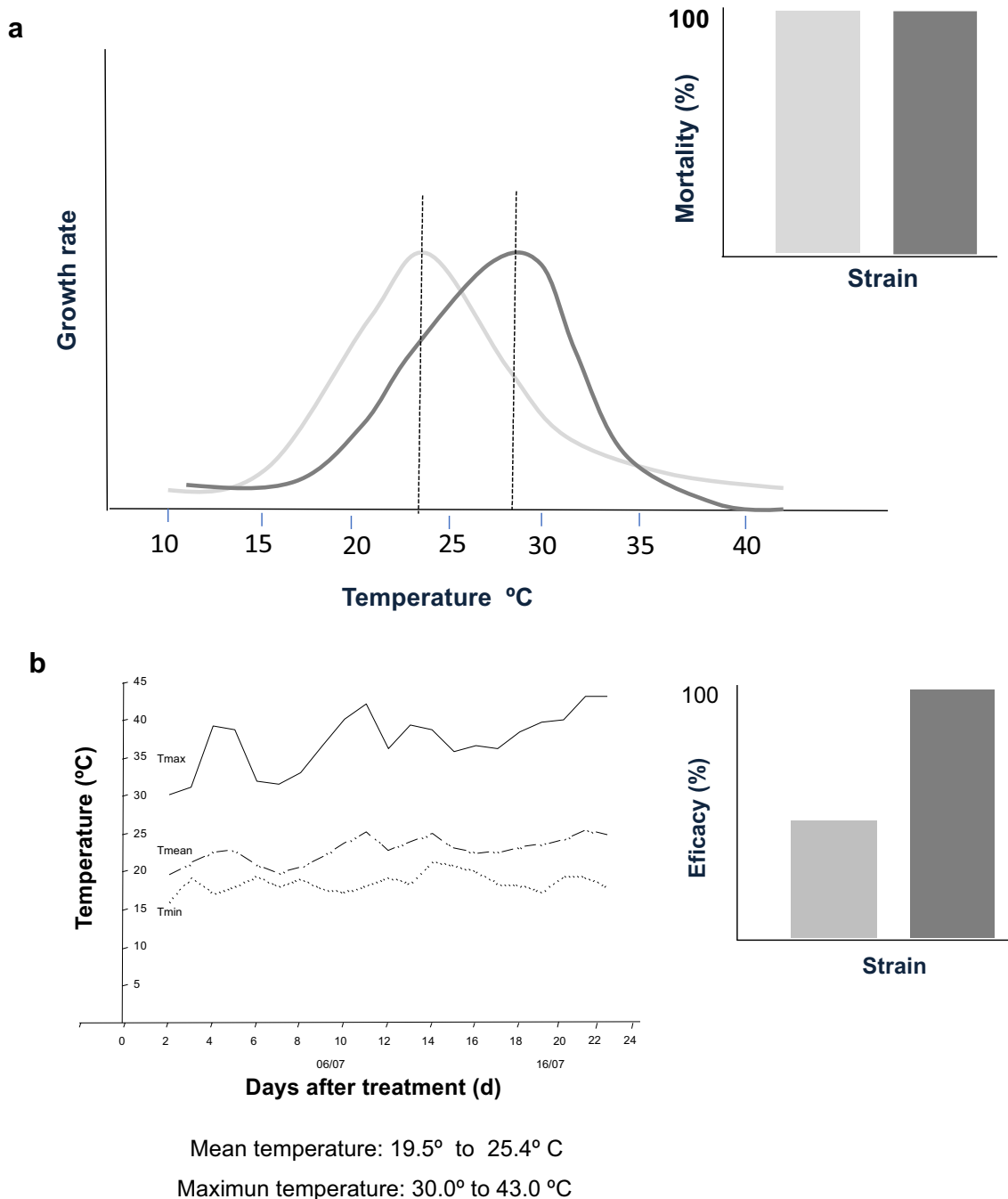
Fig. 2 Differences between laboratory and field efficacy of two entomopathogenic fungal strains due to a lack of temperature competence. **a** Laboratory efficacy of two strains against third instar larvae of *Trialeurodes vaporariorum* showing the mean temperature for growth of the two strains. **b** Efficacy of two strains in a commercial greenhouse against the same pest showing that if the temperature regime of the greenhouse during the treatment can explain the lack of environmental competence in one strain (light gray) compared with the other strain (dark gray)

mycelial growth in blue, green, red, and white light (Dias et al. 2020). Additionally, fungal growth under darkness and nutritional stress conditions always produces conidia with stronger stress tolerance than conidia produced under white light (Dias et al. 2021). *M. robertsii* and *Metarhizium acridum* (Driver & Milner) J.F. Bisch., S.A. Rehner & Humber (Ascomycota: Hypocreales) conidia produced on riboflavin-supplemented medium had increased UV-A tolerance and upregulated photoprotection and photoreactivation genes (Huarte-Bonnet et al. 2020).

It has been reported that moderate levels of biotic stress from a fungal competitor or low-nutrient conditions can enhance UV-B tolerance in *M. robertsii* conidia (Medina et al. 2020).

Different propagules of the same entomopathogenic fungal strain, such as conidia, blastospores, and microsclerotia, have different tolerances to UV-B exposure highlighting the need to investigate many formulations and propagule types early in the development of new fungal microbial control products (Corval et al. 2021). Conidia and microsclerotia generally have better tolerance to UV-B radiation than blastospores, although blastospores of some entomopathogenic fungal strains are still promising candidates for control of arthropod pests in regions where heat and UV-B are limiting environmental factors (Bernardo et al. 2020).

Several formulation technologies have been developed to improve EPF commercial products, e.g., encapsulation in biopolymers, which increases UV-B tolerance of various EPF, such as *B. bassiana* (Felizatti et al. 2021). It is possible to increase the persistence of *B. bassiana* conidia to UV radiation by formulation with natural UV-protective additives that may increase the efficacy of EPF as biocontrol agents in open-field applications, although not fully confirmed (Kaiser et al. 2019; Acheampong et al. 2020).

Selecting entomopathogenic fungal strains with greater resistance to UV-B radiation is a second strategy to counteract the detrimental effects of solar radiation. Both interand intra-specific variations in tolerance to solar radiation of EPF have been reported (Fernández-Bravo et al. 2016, 2017; Jaronski et al. 2010). Species in the genus *Metarhizium* are much more susceptible to propagule inactivation by UV-B radiation than species in the genus *Beauveria* (Fernández-Bravo et al. 2016, 2017), probably due to the presence of melanin that absorbs UV-B and acts as a sunscreen (Braga et al. 2015). It is important to note that the presence of dark green pigments in conidia of *Metarhizium* species does not necessarily translate into an increase in UV-B resistance because tolerance is achieved by the presence of melanin or melanin-like pigments which are not present in *Metarhizium* species (Tseng et al. 2011). The effect of UV-B radiation on fungal propagules is stronger when conidia are on a static, flat surfaces than when they are on insect bodies. For example, when *M. bunneum* was exposed to UV-B radiation (1.200 mW m^{-2}) on the surface of treated *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) it took 47.2 h before adult mortality rate was reduced by 50%, while only 5.6 h was needed to reduce the conidial viability on flat surfaces by 50% (Fernández-Bravo et al. 2017). This means that virulence is not affected even when conidial viability is severely reduced, demonstrating that, once propagules have reached the insect cuticle, the impact of UV-B radiation on their inactivation is not the critical factor reducing virulence of *M. brunneum* (Fernández-Bravo et al. 2017).

The molecular basis and regulatory mechanisms underlying entomopathogenic fungal resistance to solar UV radiation have been recently reviewed (Tong and Feng 2022). Several studies have demonstrated the involvement of particular genes for UV-B resistance in entomopathogenic fungal conidia such as genes involved in conidial maturation, DNA damage repair, antioxidant response, trehalose/mannitol biosynthesis, heat shock, cell wall integrity, and the MAPK/Hog 1 pathway (Tong and Feng 2022). Disruption of a C69-family cysteine dipeptidase gene enhanced tolerance to heat shock and UV-B in *M. acridum* (Li et al. 2020); an alkylsulfatase (MaAts) also played a key role in UV-B tolerance (Song et al. 2022). Other regulatory mechanisms are involved in photorepair of UV-induced DNA damage and the photoreactivation of UV-impaired conidia. For example, photoprotection was dependent not only on one or two photo-repair-required photolyases, but also two white collar proteins and other partners with similar or more important roles in photo-repair via interactions with photolyases (Tong and Feng 2022).

Whereas UV-B is the most harmful UV radiation, the percentage that reaches the hearth surface is reduced compared to UV-A. UV-A represents about 95% of total solar UV radiation, which is softer than UV-B radiation, but also could damages DNA, among other indirect effects (Jaronski 2010; Yao et al. 2010). It has been demonstrated that UV-A irradiation could generate reactive oxygen species (ROS) resulting in genetic modifications, cell toxicity, and signal pathway modification, but in a low proportion compared to UV-B radiation (Huarte-Bonnet et al. 2019; Jaronski 2010; Nascimento et al. 2010; Tong and Feng 2022; Yao et al. 2010). Braga et al. (2001a, b) demonstrated the negative effects of UV-A radiation on the germination and survival of *M. anisopliae* conidia under natural conditions, which emphasizes that the effect of UV-A radiation on EPF must not be neglected.

It has been suggested that the visible fraction of early morning light (low-UV) has a role in helping *Metarhizium* species mitigate potentially lethal damage due to intense UV radiation later in the day. This mechanism could increase *Metarhizium* environmental persistence and improve its bioinsecticide performance. The finding that visible light modulates stress biology has been discussed in the context of further work needed on *Metarhizium* ecology in natural and agricultural ecosystems (Brancini et al. 2022).

Overall, solar radiation is key to inactivation of entomopathogenic fungal propagules on epigeal leaf surfaces but has a lower impact on virulence. Selection of environmentally competent entomopathogenic fungal strains with increased resistance to UV-B should be mandatory to minimize the need for a combined formulation-based strategy.

Humidity

A range of 93–96.5% relative humidity (RH) is critical for fungal development and at least 96.5–98.5% RH is required for high conidial production on pellets or granules. Humidity influences conidial germination, final saprobic growth on cadavers, and sporulation (Fernández-Bravo et al. 2016; Jaronski 2010; Vega et al. 2012). As with tolerance to UV-B radiation, there are also inter- and intra-specific differences in RH requirements of EPF (Fernández-Bravo et al. 2016; Jaronski 2010). Optimal development of most EPF occurs if the RH is above 90–97%, and the critical water activity (aw) for conidial germination is about 0.90–0.92 aw (Fernández-Bravo et al. 2016; Jaronski 2010; Vidal and Fargues 2007).

Imbibition damage is a phenomenon characterized by the death of dehydrated conidia when immersed in water at temperatures lower than 25 °C (Faria et al. 2017). Some studies have suggested that this sort of damage depends on the conformational state of plasma membrane phase transition during the inhibition process (Echigo et al. 1966; Faria et al. 2017; Leach and Scott 1959). The transition of membrane phospholipids from gel (dried) to liquid crystalline (hydrated) phase in the presence of free water results in cell death (Faria et al. 2017).

However, it is the RH in the microclimate around the integument of insects, foliage, or soil surface in which entomopathogenic fungal infection will occur, that is critical in both protected and open crop growth systems, as this is where conidia germinate and infect their arthropod hosts (Boulard et al. 2002); RH conditions in the targeted insects' immediate habitat do not reflect the ambient RH in the air. As an example of this, similar mortality rates were obtained under moderate to low and high ambient RH in Mediterranean greenhouse conditions, suggesting that factors influencing leaf transpiration which affects local RH in the insects' microclimate are important (Fargues et al. 2003). Two commercial mycoinsecticides caused similar mortality rates in *T. vaporariorum* (46–88%) under moderate and high air RH conditions due to the microclimatic RH conditions at leaf surfaces, with plant transpiration-induced increases in humidity prevailing in the local habitat around targeted whitefly larvae (Fargues et al. 2003). Moreover, experiments to optimize greenhouse ventilation and RH control revealed that *Akanthomyces muscarius* (Petch) Spatafora, Kepler & B. Shrestha (Ascomycota: Hypocreales) was 89–96% efficient against *T. vaporariorum* under a wide range of ambient RH (60–90%) (Fargues et al. 2003).

Humidity could be a limiting factor in the control of stored-product pest insects by EPF because the food storage environment is maintained at low humidity to avoid proliferation of fungi that affect the quality of stored products (Rumbos and Athanassiou 2017; Singh and Fielke 2017). In this case, selected entomopathogenic fungal strains adapted to germination at low relative humidity could be useful.

Another entomopathogenic fungal application where water dependence is critical is when they are applied using lure-and-infect devices, because the fungal propagules are not protected in the soil or among vegetation and so are exposed to desiccation (Gutierrez-Cardenas et al. 2018). Selecting entomopathogenic fungal strains that are tolerant to desiccation and able to germinate under low RH conditions could be helpful in this situation.

Although soil habitats in agroecosystems do not commonly have low ambient humidities that might be detrimental to entomopathogenic fungal development, soils with high salinity could have an impact on water availability for entomopathogenic fungal propagules. This is because salt concentration has a significant impact on conidial germination as a consequence of osmotic stress; conidial germination is inhibited in in-vitro assays at conditions over a range of [NaCl] 7% (Perfetti et al. 2007; Thaochan et al. 2020). In addition, osmotic stress is also involved in reductions in conidial yield and virulence (Wang et al. 2014). Some fungal proteins involved in fungal virulence could also be induced by salinity (De Croos et al. 2001; Wang et al. 2014).

As with UV-B radiation, different entomopathogenic fungal propagules, e.g., conidia, blastospores, and microsclerotia, could have different responses to low ambient humidity/water stress related parameters, e.g., RH, water activity or salinity (Jackson and Payne 2007; Thaochan et al. 2020; Yousef-Yousef et al. 2022). Similarly, formulation could improve the fungal responses, development, and conidiogenesis under water stress conditions, and consequently enhance and extend their efficacy. For example, the addition of humectants such as vermiculite or glycerin to granular microsclerotial formulations facilitates absorption of water and increases activity against insects (Catão et al. 2021; Rodrigues et al. 2021).

Consequently, apart from rain events after application of entomopathogenic fungal conidia, which usually reduces fungal efficacy due to propagule removal (Jaronski 2010), and with the abovementioned exceptions, ambient humidity conditions do not have a critical impact on propagule mortality or virulence as microenvironmental humidity is usually optimal for entomopathogenic fungal infection (Fargues et al. 2005).

Effects of geographical origin and isolation habitat of entomopathogenic fungi on environmental competence

Microbes adapt to their natural habitat through physiological and ecological evolution, so using them under climatic and environmental conditions to which they are not adapted, can detract from their environmental competence (Robinson 2001). It has been shown that *B. bassiana* strains originating in the latitudes of Siberia and Kazakhstan from 65 to 43°N show high cold tolerance and growth even at 5 °C, whereas growth at this low temperature regimes is unusual in most of entomopathogenic fungal strains (Jaronski 2010; Kryukov et al. 2012). Moreover, the relationship between latitude of origin and the relative germination percentage of *M. anisopliae* strains after 2 h of wet-heat exposure at 45 °C has shown that strains from higher latitudes (from 40°S to 61°N) were more susceptible to heat (45 °C) than those from lower latitudes (19°S to 36°N) (Rangel et al. 2005). The European Mediterranean basin was invaded by the red palm weevil [*Rhynchophorus ferrugineus* Olivier (Coleoptera: Curculionidae)]. This started in southeastern Spain in 1996 and the pest was accompanied by *Beauveria* species; its presence has subsequently reported in several countries in the basin, with a possible host-mediate expansion of this EPF (González-Mas et al. 2019). Noteworthy, all strains obtained from *R. ferrugineus* specimens from Spain, France, Greece, and Israel have thermal, water, and UV-B requirements well fitted to the environmental conditions prevailing in the palm distribution area in the Mediterranean basin (González-Mas et al. 2019).

Research on possible relationships between geographical origin of EPF and their response to UV-B radiation has shown strong evidence for greater persistence and efficacy of local compared with exotic entomopathogenic fungal strains (Wu et al. 2020; Sutanto et al. 2022). Moreover, tolerance to UV radiation or high temperatures drives niche differentiation between *M. anisopliae* subclade Mani 2 (an above-ground entomopathogen) and *M. brunneum* and *M. robertsii* (associated with plant roots below ground) (Couceiro et al. 2021).

In contrast, differences in environmental competence associated with specific habitats have not been confirmed by scientific evidence yet. There is a substantial presence of EPF on phylloplanes of several herbaceous and woody plants (particularly *Beauveria* and *Metarhizium*) in various Mediterranean ecosystems (Garrido-Jurado et al. 2015). However, the response of EPF to temperature, water activity, and UV-B light does not differ among phylloplane strains and those isolated from soil collected at the same coordinates; the hypothesis that phylloplane strains,

being more exposed to unfavorable climatic conditions, could have evolved to respond more effectively, therefore, remains open (Fernández-Bravo et al. 2016). Despite this, some *B. bassiana* strains from the phylloplane have been found to respond exceptionally well to the abiotic factors typically found in arid environments, an outcome unrelated to both their genotype and their isolation habitat or ecosystem (Fernández-Bravo et al. 2016).

Therefore, geographical origin is a key factor for the development of effective environmentally competent EPF, in particular temperature- and humidity-competent entomopathogenic fungal strains. In fact, the lack of this competence in several mycoinsecticides used for microbial pest control results from the geographical origin of the fungal strain differing markedly from those of the zone where it is applied (Fig. 2).

Effects of geographical location, habitat type, management, cropping system, and soil factors on entomopathogenic fungal occurrence, distribution, and population structure have been investigated the last decades (Bidochka et al. 2001; Fernández-Bravo et al. 2021; Garrido-Jurado et al. 2015; Inglis et al. 2008; Kepler et al. 2015; Meyling and Eilenberg 2006; Quesada-Moraga et al. 2007; Steinwender et al. 2014). In Mediterranean ecosystems, intensification of management reduces the diversity of EPF, particularly of *Beauveria* complex species (the most abundant EPF genus in southern Spain); not only was this apparent in soils but also on the phylloplane of weeds and woody plants (Garrido-Jurado et al. 2015). However, Fernandez-Bravo et al. (2021) showed that, in Swiss soils, the most frequently occurring and abundant EPF were in the genus *Metarhizium*; forests harbored a particular genotypic population of *M. brunneum* that was in low abundance and diversity in the soil compared with more substantial populations in arable land and grasslands (Fernández-Bravo et al. 2021). This information reinforces the importance of selecting native strains as microbial control agents with specific environmental competence for a particular location.

Relationship between the insect host of entomopathogenic fungi and the fungal environmental competence

Environmental competence of EPF can also be influenced by specific ecological and physiological characteristics of their arthropod hosts. EPF are among the best developed and adapted microbial control agents of locusts and grasshoppers (Zhang et al. 2019). However, their infectivity can be limited by behavioral thermoregulation by their ectothermic hosts which use basking and/or selection of thermal microenvironments to maintain their body temperatures several degrees above ambient (preferred or "set point" body temperature)

(Carruthers et al. 1992; Jaronski 2010). Indeed, this thermoregulatory behavior can be more pronounced following infection with EPF, a phenomenon termed behavioral fever (Rakus et al. 2017), which is an adaptive defensive response that results in suppression of pathogen growth and enhanced performance of the host's immune system and has been described for many locust species (Blanford et al. 1998, 2000, 2001; Ouedraogo et al. 2004; Thomas et al. 2003; Valverde-García et al. 2018, 2019; Sangbaramou et al. 2018). For these reasons, temperature, as determined by environmental conditions and insect thermoregulation, is probably the main factor affecting the performance of bioinsecticides based on EPF for locust control, potentially reducing and/or delaying insect mortality (Blanford et al. 1998, 2000, 2001; Ouedraogo et al. 2004; Thomas et al. 2003; Valverde-García et al. 2018, 2019; Sangbaramou et al. 2018; Zhang et al. 2019). In response to behavioral thermoregulation, co-formulation of strains with broad overlapping temperature ranges has been proposed (Blanford et al. 1998, 2000, 2001; Ouedraogo et al. 2004; Thomas et al. 2003; Valverde-García et al. 2018, 2019).

While behavioral thermoregulation is usually associated with insect body heating to suppress fungal infection, cases of behavioral chilling have also been reported as a thermoregulatory response of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) to infection by *B. bassiana*; infected thrips increased survivorship and reproductive success by preferring areas maintained at 12 °C while uninfected thrips preferred areas maintained at 24 °C (Liu et al. 2019). Moreover, a relationship between melanization and thermoregulation has also been proposed (Li and Xia 2022) and even the possible detrimental effect of melanization on defense against fungal infection in locusts, with increasing temperature reducing cuticular melanism and immunity to *B. bassiana* infection in *Melanoplus sanguinipes* Fabricius (Orthoptera: Acrididae) (Sryley and Jaronski 2022).

The density-dependent prophylaxis in insects also illustrates how host behavior can affect entomopathogenic fungal infectivity (Elliot and Hart 2010; Wilson and Cotter 2008). This is exemplified in: density-dependent changes in *M. anisopliae* var *acridum* mortality in solitaria and gregaria phases of the desert locust, *Schistocerca gregaria* Forsskal (Orthoptera: Acrididae) (Wilson et al. 2001); decreased infectivity of *M. anisopliae* to the *Acromyrmex echinatior* Forel (Hymenoptera: Formicidae) ant and the *Zootermopsis angusticollis* Hagen (Isoptera: Archotermophsidae) termite kept with groups of nestmates compared those kept in isolation (Hughes et al. 2002; Rosengaus et al. 1998); and density-dependent melanization in the coleopteran *Tenebrio molitor* L. (Coleoptera: Tenebrionidae) where melanic *T. molitor* are three times more resistant to EPF than paler beetles (Barnes and Siva-Jothy 2000). This density-dependent melanization has also been described for *B. bassiana* against

Spodoptera Guenée (Lepidoptera: Noctuidae) species, with melanic larvae being more resistant to the fungus than the paler ones (Wilson and Cotter 2008). An understanding of how host-mediated effects on EPF affects environmental competence is key to developing strategies that minimize negative impacts on mycoinsecticide efficacy at economically acceptable rates.

Edaphic factors

While the overall occurrence, abundance, and community structure of EPF have been studied in a large variety of geographical locations as mentioned above, the heterogeneity in results is still not well understood. Many authors have demonstrated that differences in entomopathogenic fungal occurrence, abundance, and community structure in soils are not only due to climatic conditions, but also to other abiotic (physical and chemical soil parameters) and biotic (other soil organisms and/or products derived from them) factors (Fernández-Bravo et al. 2021; McGuire and Northfield 2020; Quesada-Moraga et al. 2007). Soil texture, pH, organic matter (particularly C/N ratio), bulk density, and soil skeleton, among others, have been reported as major drivers of variation in soil entomopathogenic fungal occurrence, diversity, and community structure (Fernandez-Bravo et al. 2021; Quesada-Moraga et al. 2007; Uzman et al. 2019). In fact, organic matter, particularly C/N ratio, are major predictors of EPF in soils from different locations (Fernandez-Bravo et al. 2021; Quesada-Moraga et al. 2007; Uzman et al. 2019).

However, since soil abiotic factors do not completely explain the variation of entomopathogenic fungal occurrence, abundance, and community structure in soils, it is important to also consider the contribution of biotic factors such as arthropod, plant, and microbial communities to understand entomopathogenic fungal behavior and their environmental competence. Nevertheless, there are few studies that have investigated how other organisms influence entomopathogenic fungal efficacy and persistence either after entomopathogenic fungal application, or as a natural interaction between native EPF and natural soil organisms.

It is very well known that many EPF have a broad insect host range. However, while some entomopathogenic fungal species can infect a wide spectrum of insects, in terms of families and orders, other species are very host specific, even to species level (Wang et al. 2012; Zimmermann 2007). How entomopathogenic fungal applications may affect nontarget soil arthropod communities in a particular habitat, has received little attention, but to date, no significant negative effects on nontarget soil fauna have been found (Azevedo et al. 2019; Garrido-Jurado et al. 2011). EPF dispersal does not only depend on horizontal transmission of the disease. Some arthropods have developed mechanisms to prevent fungal infections,

e.g., by grooming, which induces extra-fungal mobility in soils. Indeed, small arthropods, mainly springtails and some soil mites, are able to transport fungal conidia through the soil layers and even transmit the spores to other susceptible hosts (Dromph 2003; Zimmermann and Bode 1983).

In addition, it has been shown that EPF are able to form stable associations with plants as rhizosphere colonizers and/or endophytes (Barelli et al. 2016; Bruck 2010; Hu and St. Leger 2002; Vega et al. 2009; Wyrebek et al. 2011). Regarding the rhizosphere, recent studies have shown that the rhizosphere microenvironment has an important impact on entomopathogenic fungal persistence in soil. For example, some authors have found that densities of applied *M. anisopliae* inoculum were higher in growth media in close proximity to *Picea abies* (L.) H. Karst roots than in the bulk soil (Bruck 2005). In 2011, Fisher et al. found that only three *Metarhizium* species [*M. brunneum*, *M. robertsii*, and *M. guizhouense* Q.T. Chen & H.L. Guo (Ascomycota: Hypocreales)], naturally colonized plant roots in USA, each of them associated with particular plant roots. These results confirm the importance of entomopathogenic fungal strain selection, particularly species that are rhizosphere competent, which will enhance the probability of entomopathogenic fungal persistence and dispersion, and thus enhancement of their environmental competence.

While there have been a broad range of studies on commercialized phytosanitary products, the possible effects of entomopathogenic fungal applications on native microorganisms naturally present in soils have received much less attention; this includes interactions between them, which could be positive (e.g., enhancing the persistence of EPF) or negative (e.g., inhibiting the host infection process). Mayerhofer et al. (2019) demonstrated that inundative applications of *M. brunneum* to control *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae) did not have any significant effect on soil microbial communities and their multiple functions in the soil.

Considering the importance of edaphic organisms and their functions in ecosystems, knowledge about possible adverse effects on communities of native soil biota is important for safety but also for economic reasons, as it may have implications on benefit–cost analyses. Not only must abiotic climatic and edaphic factors be considered to ensure the success of entomopathogenic fungal applications, but also other communities of organisms must be taken into account for further selections of environmental competent entomopathogenic fungal strains.

Conclusions and future perspectives

Temperature is the key factor limiting infectivity of EPF, whereas UV-B, then humidity, and then temperature are the main factors causing propagule depletion. Mass production and formulation technologies can partially protect propagules from environmental inactivation, but they cannot solve the issue of the loss of virulence of entomopathogenic fungal strains. For this, the only strategy to guarantee high virulence is the selection of environmentally competent fungal strains, either from the same geographical origin/habitat, or from an area with similar climatic conditions to those of the agroecosystem where the fungus will be used. The development of microbial control solutions is increasingly convenient but has been plagued by repeated examples of a lack of environmental competence. For globalization of effective microbial control agents, world systems for microbial control product approval and authorization, particularly in the EU, should be simplified to accelerate the process and to make it less time-consuming and costly to increase the availability of mycoinsecticides adapted to relatively uniform climatic zones that can be used in integrated pest management. The development of temperature-dependent models to predict spatially suitable geographical areas for deployment of particular fungal strains as a function of their thermal biology may help guarantee entomopathogenic fungal environmental competence.

Declarations

References

Acheampong M, Hill M, Moore S, Coombes C (2020) UV sensitivity of *Beauveria bassiana* and *Metarhizium anisopliae* isolates under investigation as potential biological control agents in South African citrus orchards. Fungal Biol 124:304–310. https://doi.org/10.1016/j.funbio.2019.08.009

Alali S, Mereghetti V, Faoro F, et al (2019) Thermotolerant isolates of *Beauveria bassiana* as potential control agent of insect pest in subtropical climates. PLoS ONE 14:e0211457. https://doi.org/10.1371/journal.pone.0211457

Agbessenou A, Akutse KS, Yusuf AA, Wekesa SW, Khamis FM (2021) Temperature-dependent modelling and spatial prediction reveal suitable geographical areas for deployment of two *Metarhizium anisopliae* isolates for *Tuta absoluta* management. Sci Rep 11:23346. https://doi.org/10.1038/s41598-021-02718-w

Azevedo AGC, Eilenberg J, Steinwender BM, Sigsgaard L (2019) Non-target effects of *Metarhizium brunneum* (BIPESCO 5/F 52) in soil show that this fungus varies between being compatible with, or moderately harmful to, four predatory arthropods. Biol Control 131:18–24. https://doi.org/10.1016/j.biocontrol.2019.01.002

Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Symrnioudis I, Watt AD, Whittaker JB (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Glob Change Biol 8:1–16. https://doi.org/10.1046/j.1365-2486.2002.00451.x

Barelli L, Moonjely S, Behie SW, Bidochka MJ (2016) Fungi with multifunctional lifestyles: Endophytic insect pathogenic fungi. Plant Mol Biol 90:657–664. https://doi.org/10.1007/s11103-015-0413-z

Barnes AI, Siva-Jothy MT (2000) Density-dependent prophylaxis in the mealworm beetle *Tenebrio molitor* L (Coleoptera: Tenebrionidae): cuticular melanization is an indicator of investment in immunity. Proc R Soc Lond B Biol Sci 267:177–182. https://doi.org/10.1098/rspb.2000.0984

Bebber DP, Ramotowski MAT, Gurr SJ (2013) Crop pests and pathogens move polewards in a warming world. Nat Clim Change 3:985–988. https://doi.org/10.1038/nclimate1990

Bernardo C, Pereira-Junior R, Luz C, Mascarin G, Kamp Fernandes É (2020) Differential susceptibility of blastospores and aerial conidia of entomopathogenic fungi to heat and UV-B stresses. Fungal Biol 124:714–722. https://doi.org/10.1016/j.funbio.2020.04.003

Bidochka MJ, Kamp AM, Lavender TM, Dekoning J, De Croos JNA (2001) Habitat association in two genetic groups of the insect-pathogenic fungus *Metarhizium anisopliae*: uncovering cryptic species? Appl Environ Microbiol 67:1335–1342. https://doi.org/10.1128/AEM.67.3.1335-1342.2001

Blanford S, Thomas MB (2000) Thermal behavior of two acridid species: effects of habitat and season on body temperature and the potential impact on biocontrol with pathogens. Environ Entomol 29:1060–1069. https://doi.org/10.1603/0046-225X-29.5.1060

Blanford S, Thomas MB (2001) Adult survival, maturation, and reproduction of the desert locust *Schistocerca gregaria* infected with the fungus *Metarhizium anisopliae* var *acridum*. J Invertebr Pathol 78:1–8. https://doi.org/10.1006/jipa.2001.5031

Blanford S, Thomas MB, Langewald J (1998) Behavioral fever in the Senegalese grasshopper, *Oedaleus senegalensis*, and its implications for biological control using pathogens. Ecol Entomol 23:9–14. https://doi.org/10.1046/j.1365-2311.1998.00104.x

Boulard T, Mermier M, Fargues J, Smits N, Rougier M, Roy JC (2002) Tomato leaf boundary layer climate: implications for microbiological whitefly control in greenhouses. Agric for Meteorol 110:159–176. https://doi.org/10.1016/S0168-1923(01)00292-1

Braga GUL, Flint SD, Messias CL, Anderson AJ, Roberts DW (2001a) Effect of UV-B on conidia and germlings of the entomopathogenic hyphomycete *Metarhizium anisopliae*. Mycol Res 105:874–882. https://doi.org/10.1017/S0953756201004270

Braga GUL, Flint SD, Miller C, Anderson AJ, Roberts DW (2001b) Both solar UVA and UVB radiation impair conidial culturability and delay germination in the entomopathogenic fungus *Metarhizium anisopliae*. Photochem Photobiol 74:734. https://doi.org/10.1562/0031-8655(2001)074%3c0734:BSUAUR%3e2.0.CO;2

Braga GU, Rangel DE, Fernandes EK, Flint SD, Roberts DW (2015) Molecular and physiological effects of environmental UV radiation on fungal conidia. Curr Gent 61:405–425. https://doi.org/10.1007/s00294-015-0483-0

Brancini G, Hallsworth J, Corrochano L, Braga G (2022) Photobiology of the keystone genus *Metarhizium*. J Photochem Photobiol B Biol 226:112374. https://doi.org/10.1016/j.jphotobiol.2021.112374

Bruck DJ (2005) Ecology of *Metarhizium anisopliae* in soilless potting media and the rhizosphere: Implications for pest management. Biol Control 32:155–163. https://doi.org/10.1016/j.biocontrol.2004.09.003

Bruck DJ (2010) Fungal entomopathogens in the rhizosphere. Biocontrol 55:103–112. https://doi.org/10.1007/978-90-481-3966-8_8

Carruthers RI, Larkin TS, Firstencel H, Feng Z (1992) Influence of thermal ecology on the mycosis of a rangeland grasshopper. Ecology 73:190–204. https://doi.org/10.2307/1938731

Catão AML, Rodrigues J, Marreto RN, Mascarin GM, Fernandes ÉKK, Humber RA, Luz C (2021) Optimization of granular formulations of *Metarhizium humberi* microsclerotia with humectants. J Basic Microbiol 61:808–813. https://doi.org/10.1002/jobm.202100171

Corval A, Mesquita E, Corrêa T, Silva C, Bitencourt R, Fernandes É, Bittencourt V, Roberts D, Gôlo P (2021) UV-B tolerances of conidia, blastospores, and microsclerotia of *Metarhizium* spp. entomopathogenic fungi. J Basic Microbiol 61:15–22. https://doi.org/10.1002/jobm.202000515

Couceiro JC, Fatoretto MB, Demétrio CGB, Meyling NV and Delalibera I Jr (2021) UV-B radiation tolerance and temperature-dependent activity within the entomopathogenic fungal genus *Metarhizium* in Brazil. Front Fungal Biol 2:645737. https://doi.org/10.3389/ffunb.2021.645737

De Croos JNA, Bidochka MJ (2001) Cold-induced proteins in cold-active isolates of the insect-pathogenic fungus *Metarhizium anisopliae*. Mycol Res 105:868–873. https://doi.org/10.1017/S0953756201004099

Delcour I, Spanoghe P, Uyttendaele M (2015) Literature review: Impact of climate change on pesticide use. Food Res Int 68:7–15. https://doi.org/10.1016/j.foodres.2014.09.030

Días L, Pedrini N, Braga G, Ferreira P, Pupin B, Araújo C, Corrochano L, Rangel D (2020) Outcome of blue, green, red, and white light on *Metarhizium robertsii* during mycelial growth on conidial stress tolerance and gene expression. Fungal Biol 124:263–272. https://doi.org/10.1016/j.funbio.2019.04.007

Dias L, Souza R, Pupin B, Rangel D (2021) Conidiation under illumination enhances conidial tolerance of insect-pathogenic fungi to environmental stresses. Fungal Biol 125:891–904. https://doi.org/10.1016/j.funbio.2021.06.003

Dromph KM (2003) Collembolans as vectors of entomopathogenic fungi. Pedobiologia 47:245–256. https://doi.org/10.1078/0031-4056-00188

Echigo A, Fujita T, Kola S (1966) Relationship between biological and physical properties of dry yeast cells. J Gen Appl Microbiol 12:91–99. https://doi.org/10.2323/jgam.12.91

Eilenberg J (2006) Concepts and visions of biological control. In: Eilenberg J, Hokkanen HMT (eds) An Ecological and Societal Approach to Biological Control. Springer, Dordrecht, pp 1–11

Elliot SL, Hart AG (2010) Density-dependent prophylactic immunity reconsidered in the light of host group living and social behavior. Ecology 91:65–72. https://doi.org/10.1890/09-0424.1

Fargues J, Vidal C, Smits N, Rougier M, Boulard T, Mermier M, Nicot P, Reich P, Jeannequin B, Ridray G, Lagier J (2003) Climatic factors on entomopathogenic hyphomycetes infection of *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae) in Mediterranean glasshouse tomato. Biol Control 28:320–331. https://doi.org/10.1016/S1049-9644(03)00097-5

Fargues J, Smits N, Rougier M, Boulard T, Ridray G, Lagier J, Jeannequin B, Fatnassi H, Mermier M (2005) Effect of microclimate heterogeneity and ventilation system on entomopathogenic hyphomycete infection of *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae) in Mediterranean greenhouse tomato. Biol Control 32:461–472. https://doi.org/10.1016/j.biocontrol.2004.12.008

Felizatti,A, Manzano R, Rodrigues I, da Silva M, Fernandes J, Forim M (2021) Encapsulation of *B. bassiana* in biopolymers: improving microbiology of insect pest control. Front Microbiol 12:704812. https://doi.org/10.3389/fmicb.2021.704812

Faria M, Martins I, Souza DA, Mascarin GM, Lopes R (2017) Susceptibility of the biocontrol fungi *Metarhizium anisopliae* and *Trichoderma asperellum* (Ascomycota: Hypocreales) to imbibitional damage is driven by conidial vigor. Biol Control 107:87–94. https://doi.org/10.1016/j.biocontrol.2017.01.015

Fernández-Bravo M, Flores-León A, Calero-López S, Gutiérrez-Sánchez F, Valverde-García P, Quesada-Moraga E (2017) UV-B radiation-related effects on conidial inactivation and virulence against *Ceratitis capitata* (Wiedemann) (Diptera; Tephritidae) of phylloplane and soil *Metarhizium* sp. Strains J Invertebr Pathol 148:142–151. https://doi.org/10.1016/j.jip.2017.06.012

Fernández-Bravo M, Garrido-Jurado I, Valverde-García P, Enkerli J, Quesada-Moraga E (2016) Responses to abiotic environmental stresses among phylloplane and soil isolates of *Beauveria bassiana* from two holm oak ecosystems. J Invertebr Pathol 141:6–17. https://doi.org/10.1016/j.jip.2016.09.007

Fernández-Bravo M, Gschwend F, Mayerhofer J, Hug A, Widmer F, Enkerli J (2021) Land-use type drives soil population structures of the entomopathogenic fungal genus *Metarhizium*. Microorganisms 25:1380. https://doi.org/10.3390/microorganisms9071380

García-Fernández P, Santiago-Álvarez C, Quesada-Moraga E (2008) Pathogenicity and thermal biology of mitosporic fungi as potential microbial control agents of *Varroa destructor* (Acari: Mesostigmata), an ectoparasitic mite of honey bee, *Apis mellifera* (Hymenoptera: Apidae). Apidologie 39:662–673. https://doi.org/10.1051/apido:2008049

Garrido-Jurado I, Fernández-Bravo M, Campos C, Quesada-Moraga E (2015) Diversity of entomopathogenic Hypocreales in soil and phylloplane of five Mediterranean cropping systems. J Invertebr Pathol 130:97–106. https://doi.org/10.1016/j.jip.2015.06.001

Garrido-Jurado I, Ruano F, Campos M, Quesada-Moraga E (2011) Effects of soil treatments with entomopathogenic fungi on soil dwelling non-target arthropods at a commercial olive orchard. Biol Control 59:239–244. https://doi.org/10.1016/j.biocontrol.2011.07.001

González-Mas N, Ortega-García L, Garrido-Jurado I, Dembilio O, Jaques JA, Quesada-Moraga E (2019) Which came first: The disease or the pest? Is there a host mediated spread of *Beauveria bassiana* (Ascomycota: Hypocreales) by invasive palm pests? J Invertebr Pathol 162:26–42. https://doi.org/10.1016/j.jip.2019.01.007

Gutierrez-Cardenas OG, Cortez-Madrigal H, Malo EA, Rineaud-Nord (2018) Sex pheromone and entomopathogenic fungi: a plus in its use in the integrated pest management. Biotecnia 20:28–34. https://doi.org/10.18633/biotecnia.v20i3.707

Han JO, Naeger NL, Hopkins BK, Sumerlin D, Stamets PE, Carris LM, Sheppard WS (2021) Directed evolution of *Metarhizium* fungus improves its biocontrol efficacy against *Varroa* mites in honey bee colonies. Sci Rep 11:10582. https://doi.org/10.1038/s41598-021-89811-2

Hillocks RJ (2012) Farming with fewer pesticides: EU pesticide review and resulting challenges for UK agriculture. Crop Prot 31:85–93. https://doi.org/10.1016/j.cropro.2011.08.008

Hu G, St. Leger J, (2002) Field studies using a recombinant mycoinsecticide (*Metarhizium anisopliae*) reveal that it is rhizosphere competent. Appl Environ Microbiol 68:6383–6387. https://doi.org/10.1128/AEM.68.12.6383-6387.2002

Huarte-Bonnet C, Mannino MC, Pedrini N (2019) Oxidative stress in entomopathogenic fungi and its potential role on mycoinsecticide enhancement. In: Khan MdA, Ahmad W (eds) Microbes for Sustainable Insect Pest Management: An Eco-friendly Approach. Volume 1. Springer International Publishing, Cham, pp 197–205.

Huarte-Bonnet C, Pereira-Junior RA, Paixão FRA, Braga GUL, Roberts DW, Luz C, Pedrini N, Fernandes ÉKK (2020) *Metarhizium robertsii* and *M. acridum* conidia produced on riboflavin-supplemented medium have increased UV-A tolerance and upregulated photoprotection and photoreactivation genes. BioControl 65(2):211–222

Hughes WOH, Eilenberg J, Boomsma JJ (2002) Trade-offs in group living: transmission and disease resistance in leaf-cutting ants. Proc R Soc Lond B Biol Sci 269:1811–1819. https://doi.org/10.1098/rspb.2002.2113

Inglis GD, Duke GM, Goettel MS, Kabaluk JT (2008) Genetic diversity of *Metarhizium anisopliae* var. *anisopliae* in southwestern British Columbia. J Invertebr Pathol 98:101–113. https://doi.org/10.1016/j.jip.2007.12.001

Jackson TA, O'Callaghan M (1997) Environmental competence-an essential characteristic of successful microbial control agents for soil dwelling pests. In: Robertson LN (ed) Roberts DJ. Bureau of Sugar Experiment Stations, Brisbane, pp 74–77

Jackson TA, Alves SB, Pereira RM (2000) Success in biological control of soil-dwelling insects by pathogens and nematodes. In: Gurr G, Wratten S (eds) Biological Control: Measures of Success. Springer, Dordrecht. https://doi.org/10.1007/978-94-011-4014-0_9

Jackson MA, Payne AR (2007) Evaluation of the desiccation tolerance of blastospores of *Paecilomyces fumosoroseus* (Deuteromycotina: Hyphomycetes) using a lab-scale, air-drying chamber with controlled relative humidity. Biocontrol Sci Technol 17:709–719. https://doi.org/10.1080/09583150701527235

Jackson MA, Dunlap CA, Jaronski ST (2010) Ecological considerations in producing and formulating fungal entomopathogens for use in insect biocontrol. Biocontrol 55:129–145. https://doi.org/10.1007/s10526-009-9240-y

Jaronski ST (2010) Ecological factors in the inundative use of fungal entomopathogens. Biocontrol 55:159–185. https://doi.org/10.1007/s10526-009-9248-3

Kaiser D, Bacher S, Mène-Saffrané L, Grabenweger G (2019) Efficiency of natural substances to protect *Beauveria bassiana*

conidia from UV radiation. Pest Manag Sci 75:556–563. https://doi.org/10.1002/ps.5209

Kamga SF, Ndjomatchoua FT, Guimapi RA, Klingen I, Tchawoua C, Hjelkrem AGR, Thunes KH, Kakmeni FM (2022) The effect of climate variability in the efficacy of the entomopathogenic fungus *Metarhizium acridum* against the desert locust *Schistocerca gregaria*. Sci Rep 12:7535. https://doi.org/10.1038/s41598-022-11424-0

Kepler RM, Ugine TA, Maul JE, Cavigelli MA, Rehner SA (2015) Community composition and population genetics of insect pathogenic fungi in the genus *Metarhizium* from soils of a long-term agricultural research system. Environ Microbiol 8:2791–2804. https://doi.org/10.1111/1462-2920.12778

Kryukov VY, Yaroslavtseva ON, Elisaphenko EA, Mitkovets PV, Lednev GR, Duisembekov BA, Zakian SM, Glupov VV (2012) Change in the temperature preferences of *Beauveria bassiana* sensu lato isolates in the latitude gradient of Siberia and Kazakhstan. Microbiology 81:453–459. https://doi.org/10.1134/S0026261712041X

Leach R, Scott W (1959) The influence of rehydration on the viability of dried micro-organisms. J Gen Microbiol 2:295–307. https://doi.org/10.1099/00221287-21-2-295

Li J, Guo M, Cao Y, Xia Y (2020) Disruption of a C69-family cysteine dipeptidase gene enhances heat shock and UV-B tolerances in *Metarhizium acridum*. Front Microbiol 11:849. https://doi.org/10.3389/fmicb.2020.00849

Li J, Xia Y (2022) Host–Pathogen Interactions between *Metarhizium* spp. and Locusts. J. Fungi 8:602. https://doi.org/10.3390/jof8060602

Liu X, Reitz SR, Lei Z, Wang H (2019) Thermoregulatory response of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) to infection by *Beauveria bassiana*, and its effect on survivorship and reproductive success. Sci Rep 9:13625. https://doi.org/10.1038/s41598-019-49950-z

López Plantey R, Papura D, Couture C, Thiéry D, Pizzuolo PH, Bertoldi V, Lucero GS (2019) Characterization of entomopathogenic fungi from vineyards in Argentina with potential as biological control agents against the European grapevine moth *Lobesia botrana*. Biocontrol 64:501–511. https://doi.org/10.1007/s10526-019-09955-z

Maina UM, Galadima IB, Gambo FM, Zakaria D (2018) A review on the use of entomopathogenic fungi in the management of insect pests of field crops. J Entomol Zool Stud 6:27–32

Mann AJ, Davis TS (2020) Plant secondary metabolites and low temperature are the major limiting factors for *Beauveria bassiana* (Bals.-Criv.) Vuill. (Ascomycota: Hypocreales) growth and virulence in a bark beetle system. Biol Control 141:104130. https://doi.org/10.1016/j.biocontrol.2019.104130

Mayerhofer J, Rauch H, Hartmann M, Widmer F, Gschwend F, Strasser H, Leuchtmann A, Enkerli J (2019) Response of soil microbial communities to the application of a formulated *Metarhizium brunneum* biocontrol strain. Biocontrol Sci Technol 29:547–564. https://doi.org/10.1080/09583157.2019.1566953

McGuire AV, Northfield TD (2020) Tropical occurrence and agricultural importance of *Beauveria bassiana* and *Metarhizium anisopliae*. Front Sustain Food Syst 4:6. https://doi.org/10.3389/fsufs.2020.00006

Medina E, Oliveira A, Medina H, Rangel D (2020) Serendipity in the wrestle between *Trichoderma* and *Metarhizium*. Fungal Biol 124:418–426. https://doi.org/10.1016/j.funbio.2020.01.002

Membang G, Ambang Z, Mahot HC, Kuatea AF, Mokpkpo KK, Hannaa FR (2021) Thermal response and horizontal transmission of cameroonian isolates of the entomopathogenic fungi *Beauveria bassiana* and *Metarhizium anisopliae* – Candidates for microbial controls of the banana root borer *Cosmopolites sordidus*. Fungal Ecol 50:101042. https://doi.org/10.1016/j.funeco.2021.101042

Meyling NV, Eilenberg J (2006) Isolation and characterisation of *Beauveria bassiana* isolates from phylloplanes of hedgerow vegetation. Mycol Res 110:188–195. https://doi.org/10.1016/j.mycres.2005.09.008

Muniz ER, Paixão FRS, Barreto LP, Luz C, Arruda W, Angelo IC, Fernandes EKK (2020) Efficacy of *Metarhizium anisopliae* conidia in oil-in-water emulsion against the tick *Rhipicephalus microplus* under heat and dry conditions. Biocontrol 65:339–351. https://doi.org/10.1007/s10526-020-10002-5

Nascimento É, Da Silva SH, Dos Reis ME, Roberts DW, Braga GUL (2010) Quantification of cyclobutane pyrimidine dimers induced by UVB radiation in conidia of the fungi *Aspergillus fumigatus*, *Aspergillus nidulans*, *Metarhizium acridum* and *Metarhizium robertsii*. Photochem Photobiol 86:1259–1266. https://doi.org/10.1111/j.1751-1097.2010.00793.x

Onsongo SK, Gichimu BM, Akutse KS, Dubois T, Mohamed SA (2019) Performance of three isolates of *Metarhizium anisopliae* and their virulence against *Zeugodacus cucurbitae* under different temperature regimes, with global extrapolation of their efficiency. InSects 10:270. https://doi.org/10.3390/insects10090270

Ouedraogo RM, Goettel MS, Brodeur J (2004) Behavioral thermoregulation in the migratory locust: a therapy to overcome fungal infection. Oecologia 138:312–319. https://doi.org/10.1007/s00442-003-1431-0

Paixão FRS, Fernandes ÉKK, Pedrini N (2019) Thermotolerance of fungal conidia. In: Khan MdA, Ahmad W (eds) Microbes for Sustainable Insect Pest Management: An Eco-friendly Approach - Volume 1. Springer International Publishing, Cham, pp 185–196.

Perfetti DJC, Moreno PM, Quintero MEA (2007) Effects of thermal, saline and pH gradients on in vitro germination of a native isolate of *Beauveria bassiana* (Balsamo) Vuillemin, pathogenic to *Rhodnius prolixus* and *Triatoma maculata*. Rev Cient 17:627–631

Quesada-Moraga E (2011) Plagas de insectos y el cambio climático. Phytoma 232:21–29

Quesada-Moraga E, Navas-Cortés JA, Maranhao EAA, Ortiz-Urquiza A, Santiago-Álvarez C (2007) Factors affecting the occurrence and distribution of entomopathogenic fungi in natural and cultivated soils. Mycol Res 111:947–966. https://doi.org/10.1016/j.mycres.2007.06.006

Quesada-Moraga E, Maranhao EAA, Valverde-García P, Santiago-Álvarez C (2006) Selection of *Beauveria bassiana* isolates for control of the whiteflies *Bemisia tabaci* and *Trialeurodes vaporariorum* on the basis of their virulence, thermal requirements and toxicogenic activity. Biol Control 36:274–287. https://doi.org/10.1016/j.biocontrol.2005.09.022

Quesada-Moraga E, Santiago-Álvarez C (2008) Hongos Entomopatógenos. In: Jacas JA, Urbaneja A (eds) Control Biológico de Plagas. Phytoma, pp 98–120.

Quesada-Moraga E, Yousef-Naef M, Garrido-Jurado I (2020) Chapter 5. Advances in the use of entomopathogenic fungi as biopesticides in suppressing crop insect pests. In: Brich N, Glare T (eds) Biopesticides for Sustainable Agriculture. Burleigh Dodds Science Publishing https://doi.org/10.19103/AS.2020.0073.05.

Rakus K, Ronsmans M, Vanderplasschen A (2017) Behavioral fever in ectothermic vertebrates. Dev Comp Immunol 66:84–91. https://doi.org/10.1016/j.dci.2016.06.027

Rangel DEN, Braga GUL, Anderson AJ, Robets DW (2005) Variability in conidial thermotolerance of *Metarhizium anisopliae* isolates from different geographic origins. J Inver Pathol 88:116–125. https://doi.org/10.1016/j.jip.2004.11.007

Robinson CH (2001) Cold adaptation in Arctic and Antarctic fungi. New Phytol 151:341–353. https://doi.org/10.1046/j.1469-8137.2001.00177.x

Rodrigues J, Catão AML, Dos Santos AS, Paixão FRS, Santos TR, Martinez JM, Marreto RN, Mascarin GM, Fernandes ÉKK,

Humber RA, Luz C (2021) Relative humidity impacts development and activity against *Aedes aegypti* adults by granular formulations of *Metarhizium humberi* microsclerotia. Appl Microbiol Biotechnol 105:2725–2736. https://doi.org/10.1007/s00253-021-11157-6

Rosengaus RB, Guldin MR, Traniello JFA (1998) Inhibitory effect of termite fecal pellets on fungal spore germination. J Chem Ecol 24:1697–1706. https://doi.org/10.1023/A:1020872729671

Rumbos CI, Athanassiou CG (2017) Use of entomopathogenic fungi for the control of stored-product insects: can fungi protect durable commodities? J Pest Sci 90:839–854. https://doi.org/10.1007/s10340-017-0849-9

Sangbaramou R, Camara I, Huang XZ, Shen J, Tan SQ, Shi WP (2018) Behavioral thermoregulation in *Locusta migratoria manilensis* (Orthoptera: Acrididae) in response to the entomopathogenic fungus. Beauveria Bassiana Plos One 13:19. https://doi.org/10.1371/journal.pone.0206816

Santiago-Álvarez C, Quesada-Moraga E, Valverde-García P, Román F, Chaves M, Rodríguez A (2002) Desarrollo de un formulado comercial a base de *Beauveria bassiana* para el control de insectos de interés agrícola. XIII Symposium Internacional Phytoma: Control Biológico de Plagas y Enfermedades Mediante Microorganismos y Entomófagos: Una Alternativa actual, con Potencial de Futuro. Phytoma 144:178–179

Savary S, Willocquet L, Pethybridge SJ, Esker P, McRoberts N, Nelson A (2019) The global burden of pathogens and pests on major food crops. Nat Ecol Evol 430:430–439. https://doi.org/10.1038/s41559-018-0793-y

Seid AM, Fredensborg BL, Steinwender BM, Meyling N (2019) Temperature-dependent germination, growth and co-infection of *Beauveria* spp. isolates from different climatic regions. Biocontrol Sci Technol 29:411–426. https://doi.org/10.1080/09583157.2018.1564812

Shang Y, Duan Z, Huang W, Gao Q, Wang C (2012) Improving UV resistance and virulence of *Beauveria bassiana* by genetic engineering with an exogenous tyrosinase gene. J Invert Pathol 109:105–109. https://doi.org/10.1016/j.jip.2011.10.004

Singh CB, Fielke JM (2017) Recent developments in stored grain sensors, monitoring and management technology. IEEE Instrum 20:32–55. https://doi.org/10.1109/MIM.2017.7951690

Skendžić S, Zovko M, Pajač Živković I, Lešić V, Lemić D (2021) Effect of climate change on introduced and native agricultural invasive insect pests in Europe. InSects 12:985. https://doi.org/10.3390/insects12110985

Stireman JO, Dyer LA, Janzen DH, Singer MS, Lill JT, Marquis RJ, Ricklets RE, Gentry GL, Hallwachs W, Coley PD, Barone JA, Greeney HF, Connahs H, Barbosa P, Morais HC, Diniz IR (2005) Climatic unpredictability and parasitism of caterpillars: implications of global warming. PNAS 102:17384–17387. https://doi.org/10.1073/pnas.0508839102

Song L, Xue X, Wang S, Li J, Jin K, Xia Y (2022) MaAts, an Alkylsulfatase, contributes to fungal tolerances against UV-B irradiation and heat-shock in *Metarhizium acridum*. J Fungi 8:270. https://doi.org/10.3390/jof8030270

Srygley RB, Jaronski ST (2022) Increasing temperature reduces cuticular melanism and immunity to fungal infection in a migratory insect. Ecol Entomol 47:109–113. https://doi.org/10.1111/een.13088

Steinwender BM, Enkerli J, Widmer F, Eilenberg J, Thorup-Kristensen K, Meyling NV (2014) Molecular diversity of the entomopathogenic fungal *Metarhizium* community within an agroecosystem. J Invertebr Pathol 123:6–12. https://doi.org/10.1016/j.jip.2014.09.002

Sutanto K, Husain M, Rasool K, Malik A, Al-Qahtani W, Aldawood A (2022) Persistency of indigenous and exotic entomopathogenic fungi isolates under ultraviolet B (UV-B) irradiation to enhance field application efficacy and obtain sustainable control of the red palm weevil. InSects 13:133. https://doi.org/10.3390/insects13010103

Thaochan N, Benarlee R, Shekhar Prabhakar C, Hu Q (2020) Impact of temperature and relative humidity on effectiveness of *Metarhizium guizhouense* PSUM02 against longkong bark eating caterpillar *Cossus chloratus* Swinhoe under laboratory and field conditions. J Asia Pac Entomol 23:285–290. https://doi.org/10.1016/j.aspen.2020.01.006

Thomas MB, Watson EL, Valverde-Garcia P (2003) Mixed infections and insect-pathogen interactions. Ecol Lett 6:183–188. https://doi.org/10.1046/j.1461-0248.2003.00414.x

Thomson LJ, Macfadyen S, Hoffmann AA (2010) Predicting the effects of climate change on natural enemies of agricultural pests. Biol Control 52:296–306. https://doi.org/10.1016/j.biocontrol.2009.01.022

Tong SM, Feng MG (2020) Phenotypic and molecular insights into heat tolerance of formulated cells as active ingredients of fungal insecticides. Appl Microbiol Biotechnol 104:5711–5724. https://doi.org/10.1007/s00253-020-10659-z

Tong S, Feng M (2022) Molecular basis and regulatory mechanisms underlying fungal insecticides' resistance to solar ultraviolet irradiation. Pest Manag Sci 78:30–42. https://doi.org/10.1002/ps.6600

Tseng MN, Chung PC, Tzean SS (2011) Enhancing the stress tolerance and virulence of an entomopathogen by metabolic engineering of dihydroxynaphthalene melanin biosynthesis genes. Appl Environ Microbiol 77:4508–4519. https://doi.org/10.1128/AEM.02033-10

Uzman D, Pliestera J, Leyerb I, Entlingc MH, Reinekea A (2019) Drivers of entomopathogenic fungi presence in organic and conventional vineyard soils. Appl Soil Ecol 133:89–97. https://doi.org/10.1016/j.apsoil.2018.09.004

Vänninen I, Hokkanen H, Tyni-Juslin J (1999) Screening of field performance of entomopathogenic fungi and nematodes against cabbage root flies (*Delia radicum* l. and *D. floralis* (fall.); Diptera, Anthomyiidae). Acta Agric Scand - B Soil Plant Sci 49:167–183. https://doi.org/10.1080/09064719909362513

Valverde-Garcia P, Santiago-Álvarez C, Thomas MB, Garrido-Jurado I, Quesada-Moraga E (2018) Comparative effects of temperature and thermoregulation on candidate strains of entomopathogenic fungi for Moroccan locust *Dociostaurus maroccanus* control. Biocontrol 63:819–831. https://doi.org/10.1007/s10526-018-9904-6

Valverde-García P, Santiago-Álvarez C, Thomas MB, Maranhao EAA, Garrido-Jurado I, Quesada-Moraga E (2019) Sublethal effects of mixed fungal infections on the Moroccan locust, *Dociostaurus maroccanus*. J Invert Pathol 161:61–69. https://doi.org/10.1016/j.jip.2018.12.009

Vega FE, Goettel MS, Blackwell M, Chandler D, Jackson MA, Keller S, Koike M, Maniania NK, Monzon A, Ownley BH, Pell JK, Rangel DEN, Roy HE (2009) Fungal entomopathogens: new insights on their ecology. Fungal Ecol 2:149–159. https://doi.org/10.1016/j.funeco.2009.05.001

Vega FE, Meyling NV, Luangsa-ard JJ, Blackwell M (2012) Fungal entomopathogens. In: Vega FE, Kaya HK (eds) Insect Pathology. 2nd edition. Academic Press, Cambridge, pp. 171–220. https://doi.org/10.1016/B978-0-12-384984-7.00006-3

Vidal C, Fargues J, Rougier M, Smits N (2003) Effect of air humidity on the infection potential of Hyphomycetous fungi as mycoinsecticides for *Trialeurodes vaporariorum*. Biocontrol Sci Technol 13:183–198. https://doi.org/10.1080/0958315021000073457

Vidal C, Fargues J (2007) Climatic constraints for fungal bioinsecticides. In: Ekesi S, Maniania NK (eds) Use of entomopathogenic

fungi in biological pest management. Research Signpost Inc, Kerala, pp 39–55

Wang ZL, Li F, Li C, Feng MG (2014) Bbssk1, a response regulator required for conidiation, multi-stress tolerance, and virulence of *Beauveria bassiana*. Appl Microbiol Biotechnol 98:5607–5618. https://doi.org/10.1007/s00253-014-5644-4

Wang B, Kang Q, Lu Y, Bai L, Wang C (2012) Unveiling the biosynthetic puzzle of destruxins in *Metarhizium* species. Proc Natl Acad Sci 109:1287–1292. https://doi.org/10.1073/pnas.1115983109

Wilson K, Cotter SC, Reeson AF, Pell JK (2001) Melanism and disease resistance in insects. Ecol Lett 4:637–649. https://doi.org/10.1046/j.1461-0248.2001.00279.x

Wilson K, Cotter SC (2008) Density-dependent prophylaxis in insects. In: Ananthakrishnan TN, Whitman TN (eds) Insects and phenotypic plasticity. Science Publishers, Enfield, UK, pp 381–420

Wu S, Toews M, Oliveira-Hofman C, Behle R, Simmons A, Shapiro-Ilan D (2020) Environmental tolerance of entomopathogenic fungi: A new strain of *Cordyceps javanica* isolated from a whitefly epizootic versus commercial fungal strains. InSects 11:1–15. https://doi.org/10.3390/insects11100711

Wyrebek M, Huber C, Sasan RK, Bidochka MJ (2011) Three sympatrically occurring species of *Metarhizium* show plant rhizosphere specificity. Microbiology 157:2904–2911. https://doi.org/10.1099/mic.0.051102-0

Yao SL, Ying SH, Feng MG, Hatting JL (2010) In vitro and in vivo responses of fungal biocontrol agents to gradient doses of UV-B and UV-A irradiation. Biocontrol 55:413–422. https://doi.org/10.1007/s10526-009-9265-2

Yousef-Yousef M, Romero-Conde A, Quesada-Moraga E, Garrido-Jurado I (2022) Production of microsclerotia by *Metarhizium* sp., and factors affecting their survival, germination, and conidial yield. J Fungi (Basel) 8:402. https://doi.org/10.3390/jof8040402

Zhang SZ, Xia YX, Keyhani NO (2011) Contribution of the gas1 gene of the entomopathogenic fungus Beauveria bassiana, encoding a putative glycosylphosphatidylinositol-anchored beta-1,3-glucanosyltransferase, to conidial thermotolerance and virulence. Appl Environ Microbiol 77:2676–2684. https://doi.org/10.1128/AEM.02747-10

Zhang L, Lecoq M, Latchininsky A, Hunter D (2019) Locust and grasshopper management. Annu Rev Entomol 64:15–34. https://doi.org/10.1146/annurev-ento-011118-112500

Zimmermann G (2007) Review on safety of the entomopathogenic fungus *Metarhizium anisopliae*. Biocontrol Sci and Technol 17:879–920. https://doi.org/10.1080/09583150701593963

Zimmermann G, Bode E (1983) Investigations on the dispersal of the entomopathogenic fungus *Metarhizium-anisopliae* (fungi imperfecti, moniliales) by soil arthropods. Pedobiologia 25:65–71. https://doi.org/10.1016/S0038-0717(01)00130-4

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