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MODES OF ACTION OF ENTOMOPATHOGENIC FUNGI

Hacer Handan Altinok [1,*], Mahmut Alper Altinok [1], Abdurrahman Sami Koca [2]

[1] Erciyes University, Faculty of Agriculture, Department of Plant Protection, 38039 Kayseri, Turkey
[2] Bolu Abant Izzet Baysal University, Faculty of Agricultural and Natural Science, Department of Plant Protection, Bolu, Turkey

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Abstract
Commercial formulations of entomopathogenic fungi are successfully applied as an alternative to chemical agents in control of agricultural pests. One of the major properties of these species is building resting spores under unfavorable environmental conditions and having facultative or saprophytic properties. Mitosporic fungi such as Beauveria bassiana, Lecanicillium lecanii, Metarhizium anisopliae and Isaria fumosorosea are common species worldwide and capable of infect species from Lepidoptera, Hemiptera, Coleoptera and Diptera. Entomopathogenic fungi infests the host insects via digestion, respiration and through integument. In infestation from integument which is one of the most common infestation methods, fungi grows hyphae to penetrate epicuticle and progresses into hypodermis to achieve the infestation. Anamorphic fungi like B. bassiana and M. anisopliae primarily propagates as blastospores rather than hyphal development and these blastospores invade the vital organs by dispersing across the insect body via circulation of hemolymph within body cavity and eventually result in death of insect by clogging the circulatory system. The fungus moves to facultative feeding phase after death of host and initiates hyphal development outwards the integument, builds massive amount of spores. Conidiospores found on conidiophores are utilized to establish new infestations. Some entomopathogenic fungi are capable of killing the host even faster by excreting some mycotoxins (like beauvericin, cyclodepsipeptide, destruxin and desmethyldestruxin) at earlier stages of the infestations. Toxigenic fungi are able to kill the host earlier as compared to non-toxigenic species. In this study, information on the mechanisms used by entomopathogenic fungi for infestation of their hosts are presented.

Keywords: Biological control, Fungi, Mycoinsecticide, Pest management

1. INTRODUCTION

Entomopathogenic fungi have important roles in the natural regulation of many insect pests and pest populations. Several species of entomopathogenic fungi are being produced commercially and used as biological control agents against many insect pests in many parts of the world (Sevim et al., 2015). The use of pesticides against pests, disease agents and weeds in agricultural lands are problematic, which causes deterioration of natural balance and environmental pollution. In addition, it directly and indirectly affects human health negatively (Eken and Demirci, 1997). When all these issues are considered, the importance of alternative control methods and integrated management methods draw the attention (Erkılıç and Uygun, 1993).
Integrated and biological control methods emerged as an alternative to chemical control (Bora, 2002). Research on microbial control within biological and integrated control methods has started to increase (Eken and Demirci, 1997; Milner, 2000; Rumbos and Athanassiou, 2017). Today, many of

*Corresponding author, E-mail address: ahandan@gmail.com

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the fumigants used in control of storage pests are either banned or restricted. Entomopathogenic fungi from *Lecanicillium*, *Isaria* and *Beauveria* genus are reported as effective to adults of storage pests such as *Acanthoscelides obtectus* (Ondráčková, 2015). Mostly, biological control is used with the aid of various organisms or their toxic metabolites to prevent the activity of pests, disease agents and weeds in cultivated plants (Isaac, 1992). Some entomopathogenic fungi are able to kill the host even faster by excreting some mycotoxins (like beauvericin, cyclodepsipeptide, destruxin and desmethyldestruxin) at earlier stages of the infestations. Toxigenic fungi are able to kill the host earlier as compared to non-toxigenic species (Wang et al., 2018).
Entomopathogens are called as organisms that cause disease in insects. The use of microorganisms such as fungi, bacteria, viruses, rickettsia and nematodes living on harmful insects to kill them is known as microbial control (Öncüer, 1995). Entomopathogenic fungi are biological control agents. They play an important role in suppressing many pest populations (Roy et al., 2006) and used successfully in many phytophagous Arthropods in nature (epizootic) or in laboratories. Many studies have been carried out on microbial control using entomopathogenic microorganisms with biological control methods against these phytophagous species. (Alay, 1965; Zare and Gams, 2001; Kim, 2007; Demirci et al., 2008; Gurulingappa et al., 2010; Xie et al., 2010). There are more than 500 species of fungi that can infect insects (Roberts, 1981; Hall and Papierok, 1982; Zimmermann, 1986; Erkılıç and Uygun, 1993; Kılıç and Yıldırım, 2008). Entomopathogenic fungi have been identified in various parts of the world and they create an effective suppression on natural insect populations (Tanada and Kaya, 1993; McCoy et al., 1988). Some fungi species are used successfully in the biological control of various pests, disease agents and weeds in the world (Eken and Demirci, 1997).
The aim of the present review is to summarize infection mechanism of some entomopathogenic fungi and use of these fungi as mycoinsecticides.

2. ENTOMOPATHOGENIC FUNGI AND THEIR ACTION MECHANISM

The entomopathogenic fungi are used in microbial control to prevent arthropod species in cultivated lands. These fungi take place in Ascomycota, Basidiomycota, Entomophthoromycotina, Blastocladiales, Kickxellomycotina, Microsporidia and Neocallimastigomycota subdivisions (Stock et al., 2009). Table 1 shows some licensed fungus content widely used as microbial insecticides worldwide (Milner, 2000). Table 2 shows the common fungal insecticides in Turkey.

Table 1. Some common fungus-containing microbial insecticides commonly used worldwide

Fungi species	Effective Host	Commercial Name
Beauveria bassiana (Bals. Criv) Vuill.	Whiteflies, aphids, thrips	Mycotrol
B. bassiana	Sucking insects	Naturalis
Metarhizium anisopliae (Metchnikoff) Sorokin	Termits	BioBlast
Lecanicillium lecanii R. Zare & W. Gams	Aphids	Vertalec
L. lecanii	Whiteflies	Mycotal
Paecilomyces fumosoroseus (Wize) A.H.S.Br & G.Sm.	Whiteflies, thrips	PFR-97
B. brongniartii	Manas larvae	Engerlingpilz
M. anisopliae	Grasshoppers	Green Muscle
B. bassiana	Manas larvae	Betel

*Corresponding author, E-mail address: ahandan@gmail.com

Table 2. Common fungal insecticide in Turkey

Fungi species	Effective Host	Commercial Name
Metarhizium anisopliae	Whiteflies, thrips, aphids and caterpillars	MET52 EC
Metarhizium anisopliae	Whiteflies, thrips, aphids and caterpillars	MET52 G

Entomopathogenic fungi enter through the cuticle directly (Sevim et al., 2015). This process occurs partly physically and enzymatically (Erkılıç and Uygun, 1993; Clarkson and Chamley, 1996). The action mechanisms of entomopathogenic fungi; firstly, the fungus spores settle on the insect cuticle, then the spores germinate and enter the cuticle by forming appressorium. Hyphae develop in hypodermis and they continue to multiply in insect body and blood cells and cause the death of the insect. Permanent sexual and asexual periods occur with asexual spores that can spread by saprophytic development on these dead individuals (Glare and Milner, 1991).

One of the most studied subjects about entomopathogenic mechanism is toxin secretion of fungi. For example, *Beauveria bassiana* and *Metarhizium anisopliae* secrete toxin in artificial environments. These substances can cause insect death even before spread and form spores in tissue of parasitic fungus. In most cases, the digestion of fungal propagules can cause death due to toxic effect rather than mycosis (Charnley, 2003). One of the most important features of insect is parasitic fungi forms resistant to environmental conditions and they have saprophytic properties. Therefore, they can be isolated from soil and organic wastes and increase the chance of using as biological agents (Erkılıç and Uygun, 1993).

3. INFECTION FORMS ON INSECTS OF ENTOMOPATHOGENIC FUNGUS

Entomopathogenic fungi have wide range of morphologically, phylogenetically, and ecologically diverse fungal species and exhibit phylogenetic diversity that reproduce via sexual or asexual spores, or both. Entomopathogenic fungi infect host insects by digestion, respiration, and particularly through the skin. Mouth parts have great importance in infection by digestion. For example, while insecticides cannot be infected by artificial infection of *Beauveria tenella* (Delacr.) to the intestines of *Melolontha melolontha* L. larvae, the fungus can be produced by oral control (Ferron, 1978; Sevim et al., 2015).

It is known that enzymes capable of degrading the chitin-protein composition in insect skin have an important role in transdermal infection (Clarkson and Chamley, 1996). After the entomopathogenic fungus spore adheres to the skin of the insect, if the climatic conditions are favorable, it forms the germination nail and penetrates the epicuticula with the help of oil and protein degrading enzymes and reaches hypodermis. Then, these hyphae multiply and spread in the body cavity. Micelles filling the body cavity kill the insect. The fungus forms chlamydospores and keep alive in the dead insect body. These chlamydospores germinate under appropriate conditions to form conidiophores on the skin of the dead insect. The spores on conidiophores are also ready for new infections (Ferron, 1978; Shah and Pell, 2003; Goettel et al., 2005).

The fungus should reach the hypodermis in order to be successful in transdermal infection. This is very important because of molting in insects. Especially, it gets more important for insects that molting at frequent and short periods of time. If the insect molt before the fungal infection reaches to the hypodermis, it can rescue from the infection. But if the infection reaches to the hypodermis, the insect cannot rescue itself from the infection (Öncüer, 1984).

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Entomopathogenic fungi-based biopesticides including *Beauveria bassiana* and *Metarhizium anisopliae* are the most frequently used entomopathogenic fungi worldwide (Faria and Wraight, 2007).

4. IMPORTANT ENTOMOPATHOGENIC FUNGUS SPECIES

Beauveria bassiana

Beauveria bassiana (Balsamo) Vuillemin (Hypocreales: Cordycipitaceae) is the best known as an insect pathogen. The teleomorph name has been *Cordyceps bassiana*. *Beauveria bassiana* known as "white muskadin" causes to disease in insects. This fungus produced aerial conidia, single-cell blastospores by germination when they come into contact with the upper skin layer of insects and penetrate directly into the bodies of their hosts from the upper skin (Kim et al., 2010). The fungus proliferates rapidly in the body by producing toxins. Therefore, unlike bacterial and viral pathogens of insects, just a contact is sufficient for infection of *B. bassiana* and other fungus pathogens. When fungus kills its host, it evolves outward by covering the insect with a white layer of mildew. This mildew produces millions of new infective spores that released into the environment. *Beauveria bassiana* is widely distributed in nature and has a potential to control with a broad host range of approximately 700 insect species used for management of many crop insect pests. This fungus is applied as conidial sprays against insects. *B. bassiana* is used as a control agent in the field and laboratory against a large number of pests such as whiteflies, aphids. In addition, *B. bassiana* does not harm a large number of non-target organisms (Irigaray et al., 2003). Entomopathogenic fungi have a wide host range than the other biological control agents. They are known to infect Lepidoptera, Hemiptera, Coleoptera and Diptera species, and *B. bassiana*, *M. anisopliae* and *L. lecanii* are widely used worldwide (Deacon, 1983). One of the most controversial issues about entomopathogenic fungi is the secretion of toxins from these organisms. It was reported that *B. bassiana* was produced locally in China and used against *Ostrinia nubilalis* and *Dendrolimus* spp. (Erkılıç and Uygun, 1993). *B. bassiana* can be successfully used against *Leptinotarsa decemlineata* in Turkey (Çam et al., 2002).
Entomopathogenic fungi and pesticides can be used in integrated pest management (IPM) programs considering the fungus as an important pest control agent. *Beauveria bassiana* is easily used together with other chemical insecticides (Chloronicotiyl, Imidaclorid) and provides a synergistic effect in control of *Bemisia tabaci*. However, it should never be used together with commercially available fungicides (Maneb, Mancozep, Thiophanatemetihyl), because these commercial fungicides are the chemicals that inhibit the growth of mycelium of *B. bassiana* (Hoddle, 1999).
Anamorphic fungi such as *B. bassiana* and *M. anisopliae* are generally developed as biological control agents applied together against pest populations. These fungi are less likely to multiply in the biotic environment and remain in nature during their application. Therefore, studies on these fungi are related to biopesticide aspects rather than their basic ecology. Anamorphic entomopathogenic fungi naturally spread extensively, particularly in soil. However, less information is known about their feeding behavior, population structure, factors affecting their distribution, and the variation of virulence-related characters (Chandler, 2005).

Metarhizium anisopliae

Metarhizium anisopliae (Metsch) Sorok (Ascomycota: Clavicipitaceae) usually multiply in the form of blastospores or hyphae structures in their host, similar to yeasticidal and spread to the body cavity with blood fluid movement in the insect body. *M. anisopliae* is a mitosporic fungus with asexual reproduction. The spores of these fungi penetrate into the insect body by contact and kill the

*Corresponding author, E-mail address: ahandan@gmail.com

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host. They have cylindrical conidia produced and subcylindrical phialides. The disease caused by the fungus is known as green muscardine disease because of the green colour of its spores (Driver at al., 2000). It is a biological agent for use in greenhouses where bumblebees and natural enemies are present. The effectiveness of *M. anisopliae* against flower thrips (*Frankliniella occidentalis* Perg.), which is an important pest in pepper cultivation, has been investigated and found as effective as the licensed fungicides (Dura, 2010). Due to the biological origin of contact-effective *M. anisopliae*, it has no side effects on both the environment and humans.
Entomopathogenic fungi are able to colonize in plant roots as symptomless endophytes. *M. anisopliae* is both entomopathogen and endophyte in soil, insects and they can colonize in roots of a variety of plants resulting in increased plant growth and tolerance against pests and diseases (Sasan and Bidochka, 2012).

Lecanicillium lecanii

L. lecanii is an entomopathogenic fungus species, that was previously widely known as Verticillium lecanii. The spores of the *Lecanicillium lecanii* germinate and produce hyphae on insects and penetrate into the body cavity where they rapidly develop tissue destruction. The fungus entering the insect forms blastospores. Then the fungi invasion on the insect cuticle occurs and destroy the insects within 7-10 days. Dead insects have white fungal hairs (cottony appearance, ranging from white to pale yellow). When examined under a microscope, the mycelium of the fungus appears as bright white strands (Anonymous, 2018a). *L. lecanii* is the most widely used as a commercial agent. The limitation factor of the use of these preparations depends on high levels of moisture for a long time to improve their development and effectiveness. Vertalec and Mycotal are produced from blastospores of *L. lecanii* which a preparation in wettable powder (WP) formulation. Today, Vertalec is used against aphids and Mycotal is used against whiteflies as successfully in greenhouses in western European countries. It is also stated that some strains of *L. lecanii* can be used against thrips and crustaceans in greenhouses (Hall, 1985).
Studies have been carried out for the microbial control of the species in the Hyphomycetes group due to less problems in production and application of entomopathogenic fungi. As a result of these studies, preparations containing isolates of some species have reached commercially available stages (Butt et al., 1999). Entomopathogenic fungi were affected by environmental conditions during germination and penetration stages after application and limited their usage possibilities. However, advances in formulation showed that these limitations may also be overcome. Also, shape design type and setting of application period may be useful to overcome these limitations (Butt et al., 1999).

Isaria fumosorosea

Isaria fumosorosea is a common entomopathogenic fungus, formerly known as *Paecilomyces fumosoroseus*. The blastospores of *I. fumosorosea* grow when they contact with the upper skin layer of insects and thrive penetrating directly the bodies of their hosts. They completely cover the body of the pest, and finally kill the hosts (Anonymous, 2018a). *I. fumosorosea* has wide tolerance range of temperature and rapidly develop. *I. fumosorosea* has been isolated from various insect orders and soil in many regions of the world (Hummer, 1992; Smith, 1993). It has been reported to spread rapidly both nature and greenhouse conditions in 48 insect species belonging to nine insect orders.
It was reported that *I. fumosorosea* caused death of the tobacco whitefly (*Bemisia tabaci*) in nymph and adult stage both in field and greenhouses conditions. It also caused death of the greenhouse whitefly (*Trialeurodes vaporariorum*) in greenhouse conditions (Lacey et al., 1996).

*Corresponding author, E-mail address: ahandan@gmail.com

The studies show that that *I. fumosorosea* isolates have the potential in the control of greenhouse whitefly in tomatoes and the temperature of greenhouse does not restrict the growth of fungi (Gökçe and Er, 2002).

Purpureocillium lilacinum

P. lilacinum (syn: *Paecilomyces lilacinus*) has a wide habitat, including cultivated or uncultivated soils, forests, grasslands and deserts. This species can develop between 8-38°C, while the optimal temperature is 26-30°C (Anonymous, 2018b). *P. lilacinum* conidiophores form a dense mycelium. Spores germinate when there is optimal moisture and nutrients. The vegetative hyphae are 2.5-4.0 microns. Conidiophores are 400-600 microns (Anonymous, 2018b). *P. lilacinum* was firstly found on *Meloidogyne incognita* eggs in Peru. This fungus is a facultative parasite of *M. incognita* eggs and it can also infect the other *Meloidogyne* spp. species (Whitehead, 1998). *P. lilacinum* infect *M. incognita* eggs and reduce larvae emerging from these eggs. Infection occurs on *Meloidogyne* eggs by producing enzymes that break down the eggshell by the fungus. Serine protease enzymes secreted by the fungus causes structural changes in the eggshell of the nematode. About 251 isolates of *P. lilacinum* restricted the development of *Meloidogyne javanica* eggs. Thus, the number of larvae hatched decreased and a large part of larvae hatched died (Whitehead, 1998).

5. CONCLUSIONS

Chemical control is more prominent to protect against harmful insects in agricultural areas. There are many side effects of chemical control, increasing environmental toxicity and resistance to pest. In addition, chemicals cause damage to beneficial organisms, causing a loss of natural balance. In this review, entomopathogenic fungi and other studies about the issue were compiled as alternative to chemical control, environmentally friendly and not disturbing the natural balance. However, it was seen that the studies on this issue are not sufficient in Turkey. These studies should be increased and the use of entomopathogenic fungi in the practice of biopreparation should be expanded in Turkey. The information presented in this review will be the source of the studies about entomopathogens in Turkey.

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*Corresponding author, E-mail address: ahandan@gmail.com