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## **The parasite-host system as exemplified by the interactions between entomopathogenic fungi and insects**

**Słowa kluczowe:** pasożytnictwo, układ pasożyt-żywiciel, grzyby owadobójcze, kontrola biologiczna szkodników

**Key words:** parasitism, parasite-host system, entomopathogenic fungi, biological pest control

### **1. Introduction**

Parasitism is an antagonistic interaction of two organisms belonging to different species, in which one organism (parasite) lives permanently or temporarily at the expense of the other one (host). Understanding the complex relationships between the parasite and its host is one of the fundamental problems in modern ecology. These relationships are important not only at the individual or species level. Their consequences may also affect (directly or indirectly) entire ecosystems.

This review deals with parasitism of fungi on insects and describes complexity of interactions in insect-entomopathogenic fungus system. In particular, mechanisms of insect resistance to fungal infection, and the effects of fungal pathogens on other pathogens and parasitoids (multitrophic interactions) are discussed.

In nature, one of the most frequently observed examples of parasitism on insects are epizootics (the emergence of infectious disease in a given insect population, in a given time and a given site) caused by entomopathogenic fungi. Fungal epizootics are often associated

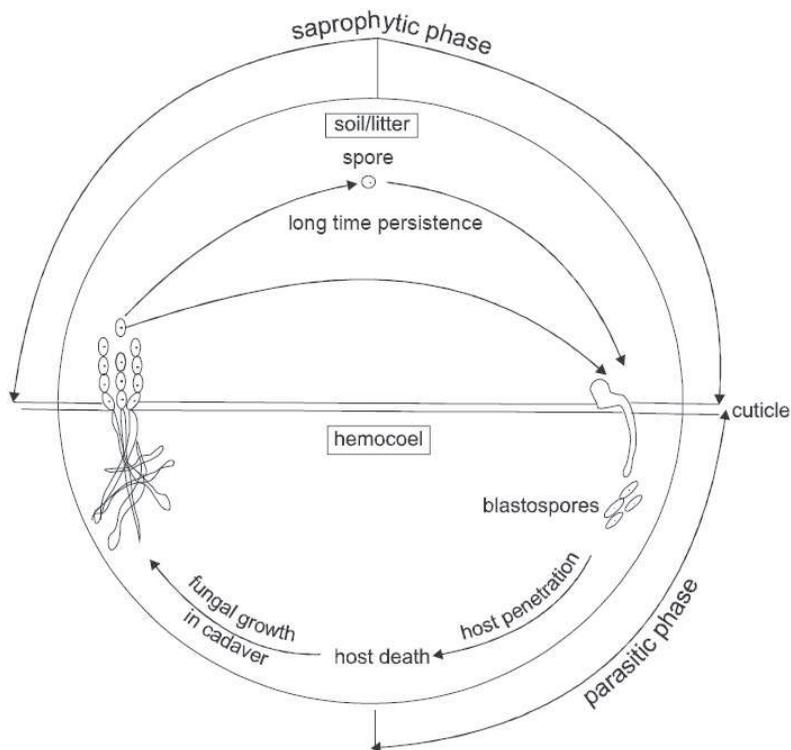
with insect-host outbreaks, i.e. rapid increase of their populations. Entomopathogenic fungi are always present in populations of insect hosts, but when density of the host population is normal infections occur sporadically. However, during insects outbreaks fungi that infect insects can increase their numbers enough to spread in the environment and contribute to the reduction of insect's population (Fuxa and Tanada 1987).

## 2. Parasitism of fungi on insects

Fungal entomopathogens occur in all habitats in which insects are present. They can be found in various taxonomic groups of fungi. However, most of them belong to the order *Hypocreales* of the phylum *Ascomycota* and to *Entomophthorales* of *Glomeromycota* (Hibbett et al. 2007).

The life cycles of these two groups of fungi are slightly different. Nevertheless, the survival and spread in the environment of both groups is dependent on the infection of the host that invariably leads to its death. Thus, parasitism of fungi on insects is an extreme example of lethal parasitism. The exceptions are *Laboulbeniales*. The *Laboulbeniales* are a unique group of fungi due to their occurrence and exploitation of the integument of living arthropods, both terrestrial and aquatic. All of the 2000 known species are considered to be obligate ectoparasites of arthropods, mainly insects. These fungi are apparently harmless to the animals they live on (Weir 2004).

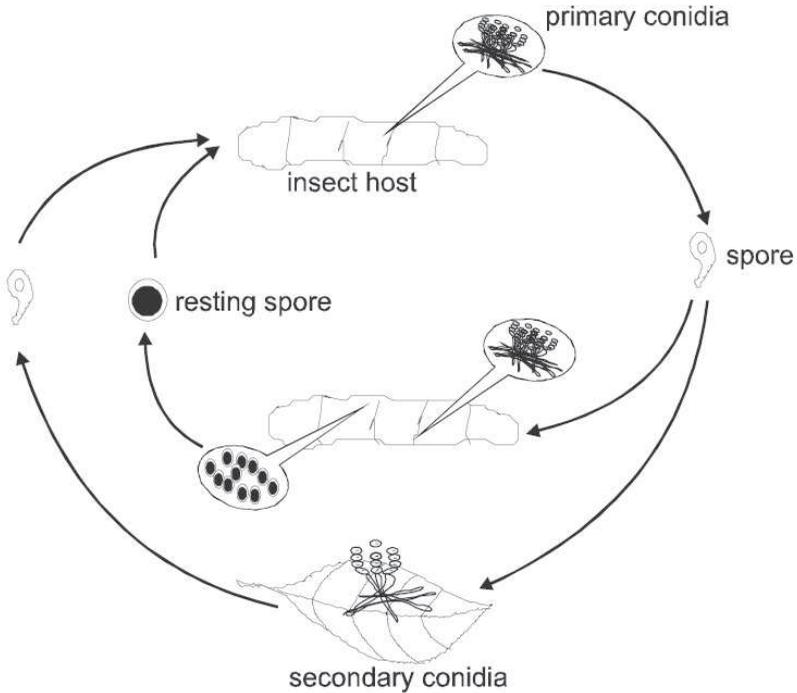
The life cycle of entomopathogenic fungus consists of a parasitic phase (from host infection to its death) and a saprophytic phase (after host death) (Fig. 1). Infection of host is usually caused by direct contact with spores that may be present on the plant surface, insect cadavers or in soil. The development of fungal infection is closely dependent on climatic conditions, particularly temperature and humidity. Entomopathogens present in the soil are also affected by its physical and chemical properties. After host death, the fungus colonizes the cadaver and during 2-3 days overgrows its cuticle and then sporulates.



**Figure 1.** The life-cycle of entomopathogenic fungi from the order *Hypocreales*

Hypocrealean fungi most often occur in nature in anamorphic (asexual =conidial) stage, whereas *Entomophthorales* produce two types of spores: asexual (primary conidia) and sexual (zygo- or azygospores) (Fig. 2). Primary conidia are produced externally on the surface of an insect after its colonization and death. If a primary conidium does not land on a new host, it germinates and forms actively ejected secondary conidia (some species can also produce tertiary and quaternary conidia). Primary conidia of *Entomophthorales* are actively discharged by hydrostatic pressure as opposed to the *Hypocreales*, which are wind dispersed. Azygospores also called resting spores to allow survi-

ve unfavourable periods or the temporary lack of hosts. In this way they synchronize their development with the development of insects (Hajek 1997).



**Figure 2.** The life-cycle of entomopathogenic fungi from the order *Entomophthorales*

### 3. Mutual adaptations

Parasite-host system is a very dynamic system linking many various adaptations and relationships that arose in the process of co-evolution. This is unquestionably the result of natural selection, which operates simultaneously on both sides of the system. Each parasite species had to evolve special adaptations that enable infection of a host and survival in it.

Entomopathogenic fungi infect their host through the external cuticle. The process of infection involves: adhesion of the spore on the insect cuticle, penetration of the cuticle by the germ tube, development of the fungus inside the insect body and colonization of the haemocoel by fungal hyphae. The spores of entomopathogenic fungi are usually covered with a layer of mucus composed of proteins and glucans, which facilitates their attachment to the insect cuticle. Germinating spores of several entomopathogenic fungi produce specialized structures called appressoria. The appressorium is responsible for attachment of germinating spore to the epicuticular surface. The process of penetration of the insect cuticle is a result of mechanical pressure and enzymatic activity of the germ tube. The major role in the penetration plays the secretion of sequential lipases, proteases and chitinases. Inside the insect body most entomopathogenic fungi grow as yeast-like propagules (blastospores), hyphal bodies or protoplasts lacking a cell wall. These structures are spread through the haemocoel. Death of an insect is usually a result of mechanical damage caused by growing mycelia inside the insect (mummification), or toxins produced and released by the pathogen (Hajek and St. Leger 1994, Hajek 1997, Bałazy 2000) (Fig. 1).

Host defenses also evolve in response to attacks by parasites. In defence against infection, insect may produce on the surface of its body fungistatic compounds that inhibit spore germination and growth. It was found that certain fatty acids on the surface of *Heliothis zea* (Lepidoptera: Noctuidae) larvae inhibit the germination of spores of *Beauveria bassiana* and *Isaria fumosorosea* (formerly *Paecilomyces fumosoroseus*). Non-pathogenic (saprophytic) fungi and bacteria occurring naturally on the insect cuticle could inhibit germination of spores of entomopathogenic fungi (Smith and Grula 1982, Saito and Aoki 1983). Insects have relatively primitive immunological system, although can react to the entrance of the fungal pathogen inside their body. Cellular defence mechanisms, such as phagocytosis or multi-haemocytic encapsulation of fungal structures, have been observed. Encapsulation is always associated with production of melanin. After infection, the fungal propagule may be encapsulated within melanin

(melanization process). Melanins act antagonistic to fungi, inhibiting their growth (Butt 1987, Hajek and St. Leger 1994, Vestergaard et al. 1999).

#### **4. Parasitic specialization, virulence and genetic diversity of the pathogen**

Close and long-term relationship and a continuous “arms race” between parasite and host causes that the parasite becomes a selective factor in the evolution of host and, conversely, that this host is the driving force behind changes in the genotype of the parasite. The parasite may be highly virulent in a new parasite-host system, but may become less virulent in a long-term system. Host, in turn, also may become more or less resistant, depending on the costs of resistance and the phylogenetic longevity of the relationship (Restif and Koella 2004).

In the population of a particular host, individuals are not equally susceptible to infection. Different species of hosts are also not equally susceptible to infection from a particular species or strain of the fungus. On the one hand, susceptibility of the host may change with its development (larvae are usually more sensitive than adults) and may depend on its behaviour. But on the other hand, different species or even strains of the fungus may display different levels of virulence and parasitic specialization against a specific host.

The question arises whether the parasitic specialization of the fungus, and thus its virulence towards particular hosts, is associated with its genetic diversity. In the case of entomopathogenic fungi with a wide range of hosts such as *Beauveria* spp. numerous studies have confirmed that the isolates of diverse geographical origin obtained from the same host species show a greater similarity in the genetic structure than the isolates from the same site but isolated from different host species (Poprawski et al. 1988, Neuvéglise et al. 1994, Cravanzola et al. 1997, Couteaudier and Viaud 1997, Maurer et al. 1997, Castrillo and Brooks 1998, Glare and Inwood 1998). For example, Maurer et al. (1997) by analysing the RFLPs (restriction fragment length polymorphism) and RAPDs (random amplification of polymorphic DNA) of 38 strains of *Beauveria bassiana* isolated from various geographi-

cal sites and from diverse species of Lepidoptera (*Ostrinia nubilalis*, *Diatraea saccharalis*, *Maliarpha separatella*) and Coleoptera (*Sitona humeralis*, *S. discoideus*), found a few homogenous groups of strains with similar genetic structure. The first group consisted of all strains isolated from *O. nubilalis*, and the second one – of strains from *D. saccharalis*. Strains isolated from *Sitona* spp. formed the third group of strains with similar genetic structure. Strains isolated from the genus *Maliarpha* gave heterogenous patterns and were not recovered as distinct groups. Furthermore, in laboratory tests, strains from *O. nubilalis* were highly virulent towards this host and less (or not) virulent against the other hosts. Similarly, Neuvéglise et al. (1994) have shown the relationship between the genetic structure of *Beauveria brongniartii* strains and their biological origins (host species). The results of PCR-RFLP revealed a perfectly homogenous group of strains isolated from *Hoplochelus marginalis* (Coleoptera: Melolonthidae). All the strains isolated from *H. marginalis* were also more virulent against this host (30-100% mortality) than the strains isolated from different insects (10% mortality). Castrillo and Brooks (1998) also found a high similarity between *B. bassiana* isolates obtained from *Alphitobius diaperinus* (Coleoptera: Tenebrionidae).

Literature data on *Metarhizium anisopliae* do not confirm such a clear relationship between genotype and specialization in relation to a particular host (Tigano-Milani et al. 1995, Fungaro et al. 1996, Bridge et al. 1997). A lot of studies indicate the crucial importance of the geographical origin of isolates (St. Leger et al. 1992, Coob and Clarkson 1993, Leal et al. 1994, Pipe et al. 1995, Leal et al. 1997, Mavridou and Typas 1998) and habitat type (Bidochka et al. 2001). Studies of Leal et al. (1994, 1997) showed that among 40 isolates of *M. anisopliae*, isolates from the same country were more similar in the genetic structure than those from different countries but the same host. Interesting observations to support a relationship between the genetic structure of *M. anisopliae* isolates and habitat type (agricultural and forested areas) along with abiotic factors (temperature and exposure to UV radiation) provides Bidochka et al. (2001). On the basis of various genetic markers (allozymes, RAPD, RFLP), they divided 83 strains of

*M. anisopliae* into two distinct groups, each associated with different habitat type. The group from forested areas showed ability for growth at low temperatures (at 8°C), while the group from the agricultural areas showed ability for growth at high temperatures (37°C) and resilience to UV exposure. The association of habitat and thermal preferences was also found for *B. bassiana* (Bidochka et al. 2002). Recently, more sensitive and reliable molecular methods enabled to find a certain association between the genetic structure of *B. bassiana* isolates and their geographical origins, but not between the genetic structure of the fungus and host systematic position (Wang et al. 2005).

Many researchers have contrasted *M. anisopliae* and *B. bassiana* as species with very different preferences and sensitivities to biotic and abiotic factors of the habitat. In general, *M. anisopliae* is considered to have higher survival rates in soil than *B. bassiana*, because it is less sensitive to adverse abiotic factors of the environment in comparison with *B. bassiana*. Strains of *Metarhizium* are also less sensitive to chemical pesticides (Doberski 1981, Bajan and Kmitowa 1982, Carruthers et al. 1985, Vänninen and Hokkanen 1988, Fargues et al. 1997). It was also found that the presence of *B. bassiana* in the soil is more dependent than that of *M. anisopliae* on the availability of hosts (Wojciechowska et al. 1977, Gotwald and Tedders 1984, Daoust and Pereira 1986, Vänninen et al. 2000). Entomopathogenic fungi as facultative parasites can survive in the soil without contact with host insects. In such conditions they are subject to various environmental factors (Lingg and Donaldson 1981, Zimmermann 1982) that may favour survivorship of certain genotypes.

## 5. Multitrophic interactions

Both components of the parasite-host system are affected, either directly (mortality, changes in growth and development) or indirectly (modifications of other biocoenosis elements), by abiotic and biotic factors. The most important biotic factor affecting herbivore insect-entomopathogenic fungus interactions are often parasitoids. Their direct impact on its host population is mainly based on limiting its

abundance, as well as changing distribution and behaviour of host individuals (Le Ralec et al. 2010). In this way parasitoids act indirectly on entomopathogenic fungi. A parasitoid and entomopathogenic fungus developing at the same time inside a host insect interact with each other by competing for resources, and the faster-growing fungus usually wins the slower developing parasitoid (Brooks 1993). Parasitoids generally increase susceptibility to infection of host insects by entomopathogenic fungi (Powell et al. 1986). However, their effect on the host, and the interactions between them, are dependent on synchronization of parasitoid attack and infection by the entomopathogenic fungus (Mesquita and Lacey 2001, Fuentes-Contreras et al 1998, Rashki et al. 2009).

Another factor that may alter biotic interactions in insect-fungus system is a host plant of an insect. Santiago-Alvarez et al. (2006) found that mortality of sweet potato whitefly, *Bemisia tabaci* (Hemiptera: Aleyrodidae), caused by *B. bassiana* was significantly affected by the host plant on which the nymphs were reared. In that study, the host plant also had a significant effect on the sporulation of the pathogen. Similar results were also obtained for other species of insects. For example, another aleyrodid, *Trialeurodes vaporariorum* (greenhouse whitefly), was more susceptible to infection caused by *Paecilomyces fumosoroseus* when fed on cucumber than on tomato (Bolckmans et al. 1995). Depending on the host plant, Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae), showed different susceptibility to infection by *B. bassiana* (Hare and Andreadis 1983). However, there are also examples showing no effect of host plant on herbivore susceptibility to infection by entomopathogenic fungi (Costa and Gaugler 1989, Vidal et al. 1998, Uguine et al. 2007). Various mechanisms may be involved in the interactions that occur in tritrophic system (pathogen-insect-host plant). In defence against herbivores, plants may produce different types of chemicals and volatile substances. These substances often can affect a pathogen directly by inhibiting its growth and germination of spores, which reduce an ability of the pathogen to infect insect (Vega et al. 1997, Lacey and Mercadier 1998, Inyang et al. 1999, Poprawski and Jones 2000, Klingner et al. 2002).

On the other hand, some substances secreted by the plant make it more or less attractive to insects and thus affect the condition of the insect, and consequently its susceptibility to infection by pathogens (Hare and Andreadis 1983, Ramoska and Todd 1985). Some microorganisms present on the surface of the host plant may also inhibit the germination of spores of entomopathogenic fungi. In addition, host plant morphology, leaf size and structure, epicuticular waxes and other features, including microclimate, which is formed on the leaf surface, are important for the interactions that occur in the system insect-entomopathogenic fungus (Inyang et al. 1998, Meekes et al. 2000). Meekes et al. (2000) studied the effect of different host plants (cucumber, poinsettia and gerbera) of the greenhouse whitefly (*Trialeurodes vaporariorum*) on germination of *Aschersonia aleyrodis* spores and mortality of whitefly nymphs. They found that on cucumber leaves, conidia stayed viable and were able to infect 90% of whitefly nymphs 31 days after spore application while on gerbera germination capacity decreased considerably (up to 50%). Mortality of whitefly nymphs was also related to their host plants. In that paper, the results discussed in the context of differences in morphology of leaves, secondary metabolites secreted by the plants, and the presence of phyllosphere microorganisms indicate the importance of host plant for the interactions between insect and pathogen. The evidence for the hypothesis that plants can use entomopathogens as bodyguards to protect themselves from herbivores has been reviewed by Elliot et al. (2000).

In the case of soil-dwelling insects, insect-fungus relationship can be modified by other soil microorganisms (viruses, bacteria, fungi) or mesofauna (nematodes). In the natural environment insects are exposed to attack by various pathogens. However, mixed infections of insects are unusual because microorganisms on the basis of antibiosis can strongly inhibit growth of other microorganisms within a host and in soil environment (Popowska-Nowak et al. 2003, Shapiro-Ilan et al. 2004, Ansari et al. 2005, Blackburn et al. 2008). Nevertheless, there are examples of co-occurrence of various fungal entomopathogens with other pathogens. Co-occurrence of fungus and virus (*Entomophaga maimaiga* and nucleopolyhedrosis virus) or two species of fungi

(*E. aulicae* and *Paecilomyces canadensis*) in natural populations of *Lymantria dispar* (Lepidoptera: Lymantriidae) has been reported (Aoki 1974, Hajek and Roberts 1992). Phenomenon of coexistence of different pathogens in natural populations of insects have been used in attempts to biological control of various pests by applying two or more pathogens in order to achieve greater mortality. Kryukov et al. (2009) found no antagonistic interaction between the entomopathogenic bacteria *Bacillus thuringiensis* and entomopathogenic fungi *B. bassiana* and *M. anisopliae* in biological control of *L. decemlineata* (Colorado potato beetle) larvae. This microbial complex was highly efficient under natural conditions causing 80-90% mortality of *L. decemlineata* larvae. Similar results were obtained for the control of *Locusta migratoria* (migratory locusts) (Orthoptera: Acrididae). A synchronous infection of the locusts with fungus *B. bassiana* (or *M. anisopliae*) and bacteria *Pseudomonas* spp., caused higher mortality of *L. migratoria* nymphs in comparison with monoinfections.  $LT_{50}$  of nymphs treated with two pathogens was shortened to three days compared with 13-17 days for the treatment with *B. bassiana* and 3-7 days for the treatment with *Pseudomonas*. Furthermore, an analysis of the dead insects showed that both pathogens could coexist in the locust (Lednev et al. 2008). Synergistic effect was also achieved with the combined application of entomopathogenic fungi and nematodes (Barbercheck and Kaya 1991, Shulte et al. 2009). However, as in the case of parasitoids, synergistic effect was achieved by postponement of application one of them. Ansari et al. (2004) have found synergistic effect against *Hoplia pилanthus* (Coleoptera: Scarabaeidae) when entomopathogenic fungus *M. anisopliae* was applied first, at least 3-4 weeks before the application of nematodes.

## 6. From theory to practice

Parasitism of fungi on insects has been used by humans in biological plant protection against pests. The first scientifically documented observation of fungal disease of insects was made by Agostino Bassi in 1835 and concerned the occurrence of *B. bassiana* in the larvae of

the silkworm moth (*Bombyx mori*) (Lepidoptera: Bombycidae). Since that time, many more or less successful attempts at introducing various fungal pathogens to the pest populations have been performed (Sandner 1971, Hajek and Dalalibera 2010).

Entomopathogenic fungi are currently most widely used in classical and inundation biological control strategies. Classical biological control is the intentional introduction and permanent establishment of an exotic biological agent for long-term pest management. Inundation biological control is the release of large numbers of mass-produced biological control agents to reduce a pest population without necessarily achieving continuing impact or establishment (Eilenberg et al. 2001).

The choice of a particular species or strain of the entomopathogenic fungus for biological control depends not only on the possibility of cheaper mass-rearing on artificial media, but mainly on its high virulence and parasitic specialization in relation to a particular host. It must also be safe for beneficial organisms (e.g. parasitoids), warm-blooded animals and humans, as well as should be characterized by a high survival in field conditions and during long-term storage. The success of field trials depends on many factors, and mainly on detailed knowledge of interactions that occur between the pathogen and the insect and the surrounding environment, as well as factors that may affect it, starting with the selection of appropriate species and strain of the fungus (Quesada-Moraga et al. 2006, Santoro et al. 2008), and ending with the way of applications (Horaczek and Viernstein 2004, Jackson et al. 2010). Better understanding of the ecology of entomopathogenic fungi is essential for more effective utilization of these organisms as microbial control agents.

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## **Układ pasożyt-żywiciel na przykładzie oddziaływań pomiędzy grzybami owadobójczym, a owadami**

### STRESZCZENIE

Pasożytnictwo to jedna z form antagonistycznego oddziaływania dwóch organizmów należących do różnych gatunków, z których jeden (pasożyt) żyje stale lub czasowo kosztem drugiego (żywiciela), będącego dla niego środowiskiem życia i źródłem pokarmu.

Zrozumienie złożonych interakcji jakie zachodzą w układzie pasożyt-żywiciel to jeden z podstawowych problemów we współczesnej ekologii. Interakcje te dotyczą nie tylko poziomu osobniczego czy gatunkowego. Mają one również wpływ (bezpośredni bądź pośredni) na całe ekosystemy.

Jednym z częściej obserwowanych w przyrodzie przejawów pasożytnictwa na owadach są epizoocje (masowe pojawienie się choroby w populacji określonego gatunku, w określonym czasie i na określonym terenie) wywoływane przez grzyby owadobójcze. W naturalnych środowiskach epizoocje grzybowe są najczęściej związane ze zjawiskiem gradacji, czyli masowym pojawieniem się owada-żywiciela. Grzyby owadobójcze, bytując w glebie czy na powierzchni roślin, są stale obecne w środowisku życia owadów, ale przy normalnym zagęszczeniu populacji owadów ich infekcje pojawiają się sporadycznie. Dopiero podczas gradacji grzyby masowo infekują owady, przyczyniając się do redukcji ich liczebności, a przy tym same zwiększają swoją liczebność i rozprzestrzenianie się w środowisku.

Przedstawiony artykuł opisuje szczegółowo interakcje jakie zachodzą w układzie grzyb owadobójczy-owad. W artykule omawiane są przystosowania grzybów owadobójczych do skutecznego infekowania żywiciela oraz mechanizmy odporności owadów na infekcje grzybowe. W pracy poruszone jest również zagadnienie współoddziaływania układu pasożyt-żywiciel z innymi elementami biocenozy (roślina żywicielska, inne patogeny, przedstawiciele wyższych poziomów troficznych), w której układ pasożyt-żywiciel funkcjonuje.