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The role of fungi in the control of grasshoppers

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Abstract: Fungi are among the most important microbial pathogens of grasshoppers with potential for development as biological control agents. Unlike most other insect pathogens that must be ingested to initiate disease, fungi generally invade insects via the external cuticle. The most common fungi that are pathogenic to grasshoppers are *Beauveria bassiana, Metarhizium anisopliae, Metarhizium flavoviride, Sorosporella* sp., and fungi in the *Entomophaga grylli* complex. A review of the latest information on the development of these fungi as microbial control agents of grasshoppers is presented. Species in the *E. grylli* complex are being used in classical biocontrol. This has resulted in controversy as there are indigenous nonpest grasshopper species that may be affected through introduction of the nonindigenous fungal strains. *Beauveria bassiana* and *M. flavoviride* are being developed for inundative control. These fungi can be mass produced and applied with equipment used for conventional pesticides. Conidia are applied either at ultralow volume in oil, as oil emulsions, or as bran-bait formulations. Field trials in Africa and North America have demonstrated significant grasshopper reductions. Improvements in formulation and inoculum targeting may further improve their efficacy.

Key words: grasshoppers, locusts, microbial control, *Beauveria bassiana, Entomophaga grylli, Metarhizium* spp.

Résumé : Les champignons comptent parmi les microorganismes pathogènes les plus importants pour les sauterelles et montrent beaucoup de potentiel pour le développement d'agents de lutte biologique. Contrairement à la plupart des pathogènes des insectes, qui doivent être ingérés pour déclencher la maladie, les champignons envahissent généralement l'insecte via ses téguments externes. Les champignons pathogènes les plus communs des sauterelles sont les *Beauveria bassiana, Metarhizium anisopliae, Metarhizium flavoviride, Sorosporella* sp., et des champignons du complexe *Entomophaga grylli*. Les auteurs présentent une revue des informations les plus récentes sur le développement de ces champignons comme agents microbiens de lutte biologique contre les sauterelles. Les agents classiques de biocontrôle appartiennent au complexe d'espèces *E. grylli*. Ceci a conduit à une controverse, parce qu'il y a des espèces de sauterelles indigènes non-visées qui peuvent être affectées par l'introduction des souches fongiques non-indigènes. On développe présentement le *B. bassiana* et le *M. flavoviride* en vue d'un contrôle massif. Ces champignons peuvent être produits en grandes quantités et appliqués avec des équipements utilisés pour les pesticides conventionnels. On applique les conidies soit à de très faibles volumes dans de l'huile, sous forme émulsifiée, ou selon la formulation sur appâts de son. Des essais aux champs, en Afrique et en Amérique du Nord, ont permis d'obtenir une diminution significative des sauterelles. Des améliorations à la formulation et au ciblage de l'inoculum pourraient encore améliorer leur efficacité.

Mots clés : sauterelles, criquets, lutte biologique, *Beauveria bassiana, Entomophaga grylli, Metarhizium* spp.
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Introduction

Grasshoppers are one of the major pests of crops worldwide. Existing control strategies rely almost exclusively on chemical insecticides. Effective alternatives to chemical insecticides that also offer improved safety could have rapid and favorable environmental and economic impact. Microbial control agents may offer an environmentally sound method for the management of grasshoppers (Goettel and Johnson 1992*a*; Prior and Greathead 1989). There were numerous efforts to use pathogens for control of grasshoppers prior to the development of chemical insecticides; however, most of these earlier efforts failed because of improper characterization of the pathogen and a general lack of understanding of epidemiology. The shortcomings of chemical pesticides have stimulated renewed interest in the microbial control of grasshoppers. Pathogens of grasshoppers include bacteria, protozoa, viruses, rickettsiae, and fungi (Bidochka and Khatchtourians 1991; Greathead 1992; Prior and Greathead 1989; Streett and Henry 1990; Streett and McGuire 1990).

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Among pathogens, fungi are probably the most important in the natural regulation of grasshopper populations, often causing widespread epizootics that decimate entire populations (Goettel 1992). Recent reviews on the development of entomopathogenic fungi as microbial control agents are those of Ferron (1985), McCoy (1990), McCoy et al. (1988), Samson et al. (1988), Tanada and Kaya (1993), and Wraight and Roberts (1987).

Unlike most other pathogens, which must be ingested in order to initiate disease, entomopathogenic fungi usually invade by penetration of the external cuticle (Charnley 1992). The infective propagule, usually a spore, attaches itself to the integument, germinates, and penetrates the host cuticle. It then grows and colonizes the haemocoel. After host death, the fungus emerges from the cadaver and, in the presence of high relative humidity, produces additional infective propagules on the surface.

There are more than 700 species of entomopathogenic fungi known worldwide; however, only a handful are known to affect grasshoppers and many of these records are based on single occurrences (Prior and Greathead 1989). Recent surveys in West Africa for hyphomycetous fungi pathogenic to grasshoppers have provided numerous new host records and some promising grasshopper control agents (Ouedraogo 1993; Shah 1994). These studies demonstrate the need for a worldwide concerted effort to isolate and characterize fungal pathogens of grasshoppers. The most common entomopathogenic fungi of grasshoppers and their natural distributions are presented in Table 1.

There are three basic approaches in microbial control that are presently being pursued against grasshoppers. The first is the classical approach, in which a pathogen is introduced to a new geographical area. With this approach, the goal is to establish the pathogen and provide long-term suppression of grasshopper populations. The second approach is the inoculative strategy, which has the goal of augmenting natural inoculum levels to initiate the spread of an epizootic. The third strategy is the inundative or microbial pesticide approach, in which the pathogen is released in large quantities with the goal of short-term suppression of a pest population.

Fungal pathogens of grasshoppers

Entomophaga grylli (Fres.) Batko (species complex)

The entomophthoralean pathogen *E. grylli* was first described from a species of cricket, and the name has been used to describe the fungus causing summit disease in grasshoppers. However, it is currently believed that the pathogens infecting grasshoppers are a complex of variant groups of species or pathotypes that differ from the type species (R.I. Carruthers, personal communication). Although several species pathogenic to grasshoppers have recently been described, the taxonomy of this group of pathogens remains unresolved. Therefore, for the purposes of this review, we will refer to this group of pathogens as the *E. grylli* complex.

Members of the *E. grylli* complex are responsible for widespread epizootics worldwide (Table 1; Carruthers and Soper 1987; Erlandson et al. 1988; Paraiso et al. 1992) and are believed to be a key factor regulating grasshopper populations in many areas, often decimating populations to below economic thresholds. For instance, in the 1960s, an epizootic of *E. grylli* in *Camnula pellucida* (Scudder) caused the near eradication of this grasshopper on the Canadian prairies (Pickford and Riegert 1964). This resulted in an 80% reduction in the required insecticide control of previous years saving approximately $30 million (N. Holmes, unpublished data). It is thought that such epizootics require high humidity with frequent dew formation; however, epizootics in very dry environments have occurred (Erlandson et al. 1988; R.S. Soper, R.A. Humber, and B. Martinell, unpublished data, cited in Soper et al. 1983).

Table 1. Host records of the most common fungal pathogens of grasshoppers.

Class and species	Geographical area
Hyphomycetes	
Beauveria bassiana	Africa, Australia, Brazil, North America
Metarhizium anisopliae	Africa, Australia, Southeast Asia, South America
Metarhizium flavoviride	Africa, North America, Galapagos Islands, Brazil
Sorosporella sp.	Africa, United States
Zygomycetes	
Entomophaga grylli (species complex)	Africa, Australia, Europe, North America, South America, Southeast Asia

Members of the *E. grylli* complex are obligate pathogens and present evidence suggests that pathotypes are relatively host specific being limited to major host groups. Infected grasshoppers climb to the top of vegetation where they firmly clasp the substrate with their heads pointing upwards and die (MacLeod 1963). Cadavers remain on the vegetation until they are dislodged by rain or wind. Soon after death of the grasshopper, some pathotypes produce only thick-walled resting spores. Other pathotypes produce either resting spores or aerial conidia. Resting spores remain dormant until suitable conditions for germination and production of conidia occur. The aerial conidia are forcibly ejected from the cadaver surface and are responsible for within-season epizootic development. If conidia land on a suitable host, they germinate and penetrate the host integument directly. If conidia land directly on a nonhost substrate, they may germinate and produce secondary or tertiary conidia, which may subsequently initiate infection in a suitable host (MacLeod 1963). If environmental conditions are not suitable for sporulation, some pathotypes are able to survive in a desiccated form; when environmental conditions become favorable, the fungus rehydrates and produces conidia within a few hours (Carruthers and Soper 1987). Free living conidia are relatively short lived, being sensitive to high temperatures, low moisture, and solar radiation (Carruthers et al. 1988; Firstencal et al. 1990).

Two biocontrol approaches, inoculative and inundative, have been attempted in recent years with members of the *E. grylli* complex. A study in New Mexico demonstrated that it may be possible to use the inoculative approach; releasing laboratory infected grasshoppers resulted in an epizootic the following year (R.I. Carruthers, personal communication).

In Alberta, resting spores held in cold storage and then exposed to light for 24 h were applied in the field in water resulting in low infection of *Melanoplus bivittatus* during the same season (D.J. Johnson, unpublished data). However, further efforts to determine the feasibility of augmentation of *E. grylli* at large scale rangeland sites are not possible as methods for the mass production of this fungus are not available.

In the classical approach, grasshoppers infected with *E. grylli* collected from North America were released in field cages in Australia containing healthy Australian grasshoppers (Milner 1985). The pathogen did not establish, even though between 5 and 30% infection occurred in the immediate area of the release sites. In contrast, an Australian pathotype of *E. grylli*, with a greater host range than North American pathotypes, has been introduced into the United States and has caused significant levels of disease among populations of three species of grasshoppers at the two release sites (R.I. Carruthers, personal communication; Carruthers and Onsager 1993).

Although no known negative environmental impacts have been observed as a result of the introduction of the Australian pathotype of *E. grylli* into the United States, concerns about the impact of this pathogen on native nontarget grasshopper species (Carruthers and Onsager 1993; Lockwood 1993) have halted further releases (R.I. Carruthers, personal communication).

There is much potential for the use of *E. grylli* fungi for microbial control of grasshoppers worldwide. However, as a start, the complex taxonomy of these species must be resolved. Development of methods for mass production of these fungi will be required if *E. grylli* is to be used as an inoculative control agent.

Beauveria bassiana (Bals.) Vuill.

This hyphomycete is a well-known and widespread insect pathogen and there have been successful attempts at developing it as an inundative microbial control agent of pest insects worldwide (Feng et al. 1994). It is cosmopolitan and various isolates are pathogenic to over 700 species of invertebrates. There are several records of *B. bassiana* infecting grasshoppers and it can cause natural epizootics in these insects (Goettel 1992; Moore and Erlandson 1988; Prior and Greathead 1989; Shah 1994).

Conidia of *B. bassiana* are borne sympodially on ampilliform conidiogenous cells. Insects generally become infected after these conidia attach to the host cuticle, germinate, and penetrate the host integument (Charnley 1992; Goettel 1992). The precise route of invasion in grasshoppers is unknown, but it is generally thought that the primary mode of infection is through the external integument. Once in the haemocoel, the fungus forms hyphal bodies or blastospores that proliferate within the insect. After host death and under moist conditions, hyphae emerge and produce a sporulating layer on the cadaver surface.

Mycotech Corporation (Butte, Mont.) is developing a strain of *B. bassiana* as a microbial control agent of grasshoppers. Initial studies with this strain showed that it is infective to grasshoppers that eat wheat leaves sprayed with conidia (Johnson et al. 1988). In other laboratory assays, it was found that two species of grasshoppers were susceptible if the fungus was applied directly to the integument or on food (leaf lettuce or wheat bran) (Goettel and Johnson 1992*b*).

The development of methods for the mass production of this strain using solid substrate technology (Bradley et al. 1992; Goettel and Roberts 1992) has facilitated field trials against grasshoppers in Canada, the United States, and Africa (C.A. Bradley and Foster, personal communication; Johnson and Goettel 1993; Johnson et al. 1992). These trials included application of *B. bassiana* conidia in an oil emulsion, in oil at ultralow volume (ULV) or in bran as carrier at rates of about 2×10^{13} conidia/ha. In some field trials, *B. bassiana* caused substantial reductions in grasshopper populations (60–93%) (C.A. Bradley, personal communication; Johnson and Goettel 1993). Other field applications have provided less promising results (C.A. Bradley, personal communication; G.D. Inglis et al., unpublished data; Johnson et al. 1992; Lobo-Lima et al. 1992).

Improvements in the formulation of conidia to increase environmental persistence and effective host contact are needed. Conidia of the Mycotech strain are relatively short lived on leaves exposed to sunlight and there was no effect of three formulations (oil, water, and oil emulsion) on conidial survival (Inglis et al. 1993). Addition of sunscreens prolonged field persistence of conidia, but it is yet to be determined if this enhanced survival will result in increased field efficacy against grasshoppers (Inglis et al. 1995). Further research on host–pathogen–environment relationships, improved formulation, and strain selection should provide information that will facilitate the development of *B. bassiana* as an inundative microbial control agent of grasshoppers.

Metarhizium anisopliae (Metsch.) Sorok. and *M. flavoviride* Gams & Rozsypal

Metarhizium anisopliae is a common insect pathogen occurring worldwide and is presently being used successfully as a microbial control agent of the sugarcane spittle bug in Brazil. Until recently, *M. flavoviride* was found mostly in certain Homoptera and it has been successfully field tested in the Philippines against the rice brown planthopper. There are numerous records of *M. anisopliae* infecting grasshoppers and it can cause natural epizootics in these insects (Goettel 1992; Prior and Greathead 1989; Shah 1994). Surveys conducted during a comprehensive collaborative research programme to develop a microbial control agent of African grasshoppers and locusts (Prior et al. 1992) revealed that *M. flavoviride* was widespread and the most common fungus pathogenic to grasshoppers in West Africa (Shah 1994). Previously, this fungus was known only from several host records in Australia and the Galapagos Islands. It has recently also been found in Brazil (B. Magalhaes, personal communication) and Madagascar (S. Jaronski, personal communication).

Although *M. anisopliae* is common in grasshoppers and causes epizootics in these insects, no highly virulent strains against grasshoppers have been identified, and therefore it has not been field tested against grasshoppers to date. In contrast, grasshopper virulent isolates of *M. flavoviride* have been identified and this fungus is being developed as a microbial control agent of grasshoppers (Prior et al. 1992;

C.J. Lomer, C. Prior, and C. Kooyman, personal communication).

As with *B. bassiana*, both species of *Metarhizium* form conidia on aerial conidiophores. The precise mode of infection is unknown, but it is generally believed that the fungus infects grasshoppers through the external integument. It has been demonstrated that *M. anisopliae* conidia ingested by desert locusts are killed by phenols present in the gut (Charnley 1992). All other aspects of pathogenesis are thought to be similar to *B. bassiana*, except that *M. flavoviride* can produce conidia within the host body cavity (B. Magalhaes, personal communication; Prior and Greathead 1989), and this may be an important factor in the epizootiology of this fungus in dry environments.

Numerous isolates of *M. flavoviride* have been tested against the desert locust (C.J. Lomer, C. Prior, and C. Kooyman, personal communication). A continuous gradation of virulence was found ranging from isolates that killed all insects within 4 days to those that were avirulent. Laboratory studies on formulation of conidia revealed that conidia formulated in oil are more efficaceous under conditions of low humidity than conidia applied in water (Bateman et al. 1993). Addition of sunscreens provided protection of conidia under laboratory conditions (Moore et al. 1993).

Development of mass production techniques amenable for use in Africa at the cottage level (N.E. Jenkins, personal communication) have facilitated field testing. *Metarhizum flavoviride* is being tested in an oil-based ULV formulation compatible with equipment for controlled droplet application (Bateman 1992). Field trials have been carried out against a variety of grasshopper species in West Africa. Field trials are also being conducted in Australia (C. Prior, personal communication) and Brazil (B. Magalhaes, personal communication). Further research is needed on field comparison of isolates from different ecozones, determination of insect–pathogen–environment relationships, and formulation of conidia to improve field efficacy.

Sorosporella sp. Sorok.

Sorosporella has been used as a form genus for some hyphomycetous fungi forming pigmented chlamydospores. Until recently, there was only one record of a *Sorosporella* from a grasshopper in Montana (R. Humber, personal communication). However, with increased interest in development of fungi as pathogens of grasshoppers, recent surveys in Africa revealed that this fungus is widespread and at times quite prevalent in several species of grasshoppers (D.L. Johnson, unpublished; S. Jaronski, personal communication; Shah 1994; B. Zelazny, personal communication). Little is known about the pathogenesis of *Sorosporella* in grasshoppers. Infected grasshoppers have been observed to regurgitate and excrete prior to death thus becoming attached to the foliage (Shah 1993). Cadavers turn brick red as a result of the body cavity becoming filled with pigmented chlamydospores. Little else is known about the epizootiology of this fungus and its potential as a control agent of grasshoppers.

Conclusions

Entomopathogenic fungi play an important role in the natural regulation of grasshopper populations worldwide. At present, entomopathogenic fungi seem to be among the most promising microbial agents for use against grasshoppers. Increased interest in the development of fungi for grasshopper control has resulted in the availability of many new isolates. Much more effort is needed to isolate fungal pathogens from grasshoppers worldwide. More effort is also needed to study fungal epizootiology, host–pathogen–environment relationships, and microbial formulation.

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