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Mini-review

Fungal entomopathogens: new insights on their ecology☆

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ABSTRACT

An important mechanism for insect pest control should be the use of fungal entomopathogens. Even though these organisms have been studied for more than 100 y, their effective use in the field remains elusive. Recently, however, it has been discovered that many of these entomopathogenic fungi play additional roles in nature. They are endophytes, antagonists of plant pathogens, associates with the rhizosphere, and possibly even plant growth promoting agents. These findings indicate that the ecological role of these fungi in the environment is not fully understood and limits our ability to employ them successfully for pest management. In this paper, we review the recently discovered roles played by many entomopathogenic fungi and propose new research strategies focused on alternate uses for these fungi. It seems likely that these agents can be used in multiple roles in protecting plants from pests and diseases and at the same time promoting plant growth.

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Introduction

Global interdependence of markets for agricultural products have increasingly brought to the forefront the need to develop agricultural practices that mitigate adverse effects on the environment and that result in products that are safe for human consumption. One major constraint to increased agricultural production is yield losses caused by insects, plant diseases, and weeds. These losses account for 40 % of potential production (Thacker 2002) and despite a marked increase in pesticide use, crop losses have remained relatively constant (Oerke 2006).

Since the late 1940s, insect pest control has relied mostly on chemical insecticides, although in many industrialized nations, pest management strategies have been shifting to the use of transgenic plants expressing particular traits such as resistance to insects, fungi, herbicides or viruses. However, the replacement of chemicals with transgenic plants does not represent a fundamental change in approach. In reality, it is a ''like-for-like'' replacement in which the tools are different but the ''silver bullet'' strategy is the same (Lewis *et al.* 1997; Welsh *et al.* 2002). A true paradigm shift would be a change from a dependence on chemicals to a total system approach (see Lewis *et al.* 1997) or to ecological engineering (see Gurr *et al.* 2004a, b). A basic component of both approaches is a better understanding of the various ecological components in an ecosystem, including biological control agents. Among these, entomopathogenic fungi have been traditionally considered as important mortality factors for insects, but recent studies discussed below have shown that they have diverse and unexpected roles. Understanding the nature of these interactions could facilitate more effective exploitation of entomopathogenic fungi for pest biocontrol strategies throughout the world, including countries where the use of other strategies might not be affordable.

The earliest studies with entomopathogenic fungi occurred in the early 1800s and concentrated on developing ways of managing diseases that were devastating the silkworm industry in France. Agostino Bassi (1773–1856) demonstrated that *Beauveria bassiana* (as *Botrytis bassiana*) was the infectious agent causing what was then known as the muscardine disease of silkworms. The stimulus for the idea of using fungal insect pathogens to manage pest insects came largely from the ensuing silkworm-disease studies, after finding that the fungus also infected other insects (Audoin 1837). Subsequently, Pasteur (1874) and LeConte (1874) suggested that fungi could be used against insects. In Russia, Elie Metchnikoff (1845–1916) conducted studies on an insect disease of wheat cockchafers that he called green muscardine, and he identified the infecting agent as *Entomopthora anisopliae* (=*Metarhizium anisopliae*). This fungus was mass-produced by Krassilstchik (1888) and used in the field against the sugar-beet weevil.

However, the discovery and use of chemical insecticides in the 1940s overshadowed the potential of entomopathogenic fungi and other microbial pest control agents, and created an inappropriate model by which the majority of microbial control agents are still judged and used, i.e., the chemical insecticides paradigm. Thus, the use of entomopathogenic fungi has not been based on an understanding of their ecology but on mistakenly applying the chemical insecticide paradigm to biological control agents and creating false expectations of chemical-like efficacy (Waage 1998).

In 1983, a group of 23 specialists in plant and insect pathology, morphology and physiology met at The Rockefeller Foundation Bellagio Study and Conference Center in Italy to discuss *Infection Processes of Fungi* (Roberts & Aist 1984). The conference was organized to afford the opportunity for in depth discussions among plant pathologists and insect pathologists. The participants recognized that there were many parallels between insect and plant pathogens as both need to invade *via* external waxy cuticular surfaces. In the following 25 y, major inroads have been made in understanding and manipulating the infection processes of insect pathogens, such as the discovery of the PR1 gene and its use in genetic modifications (St. Leger 2007). Recently, molecular tools such as DNA sequence analysis have led to a new phylogenetic classification of the fungi that has challenged many of our assumptions about the relationships among entomopathogenic and other fungi. This new phylogeny is already leading to significant new insights that should allow us to better understand the ecology of fungal entomopathogens. In addition, it has been discovered recently that many entomopathogenic fungi play additional roles in nature, including as plant endophytes, antagonists of plant pathogens, beneficial rhizosphere-associates and possibly even plant growth promoters. These findings raise two important questions: Have we been overlooking important factors in our quest to develop these microorganisms solely as biopesticides against insects? Can these agents be used in multiple roles to protect plants from insects and plant diseases and at the same time promote plant growth? Here we summarize recent findings and propose new research areas.

Entomopathogenic fungi as biopesticides

Entomopathogenic fungi are usually identified as such based on the fungal growth observed on insect cadavers. Most research on entomopathogenic fungi has been aimed at developing them as inundative biological control agents of insects, mites and ticks, despite great potential for use in conservation and classical biocontrol strategies (Butt *et al.* 2001; Goettel *et al.* 2005; Vincent *et al.* 2007). This is normally achieved through a strategy in which pest control relies on the action of the released agent but not on successive generations of the fungus. Under this paradigm, over 170 products have been developed based on at least 12 species of fungi (Faria & Wraight 2007). Despite there being an estimated 700 species of entomopathogenic fungi in approximately 90 genera (Roberts & Humber 1981), most of the commercially produced fungi are species of *Beauveria*, *Metarhizium*, *Lecanicillium* and *Isaria* that are relatively easy to mass produce. Attention has focused predominantly on the technical aspects of biopesticide development, such as mass production and formulation, and the selection of strains with rapid kill. Production requirements include reasonable cost, long-term stability and, most importantly, consistent efficacy under field conditions. The