

## Entomopathogenic fungal endophytes

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### Abstract

Fungal endophytes are quite common in nature and some of them have been shown to have adverse effects against insects, nematodes, and plant pathogens.

Our research program is aimed at using fungal endophytes-mediated plant defense as a novel biological control mechanism against the coffee berry borer, the most devastating pest of coffee throughout the world. A survey of fungal endophytes in coffee plants from Hawaii, Colombia, Mexico, and Puerto Rico has revealed the presence of various genera of fungal entomopathogens, including *Acremonium*, *Beauveria*, *Cladosporium*, *Clonostachys*, and *Paecilomyces*. Two of these, *B. bassiana* and *Clonostachys rosea*, were tested against the coffee berry borer and were shown to be pathogenic. This paper reviews the possible mode of action of entomopathogenic fungal endophytes.

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### 1. Introduction

The term endophyte was coined by the German scientist Heinrich Anton De Bary (1884), and is used to define fungi or bacteria occurring inside plant tissues without causing any apparent symptoms in the host (Wilson, 1995). Fungal endophytes have been detected in hundreds of plants, including many important agricultural commodities such as wheat (Larran et al., 2002a), bananas (Pocasangre et al., 2000; Cao et al., 2002), soybeans (Larran et al., 2002b), and tomatoes (Larran et al., 2001). Several roles have been ascribed to fungal endophytes, including providing protection against her-

bivorous insects (Breen, 1994; Clement et al., 1994), plant parasitic nematodes (West et al., 1988; Elmi et al., 2000), and plant pathogens (White and Cole, 1986; Dingle and McGee, 2003; Wicklow et al., 2005).

Most reports on the effects of endophytes on insect herbivores have concentrated on turf and agronomic grasses infected with endophytic clavicipitalean fungi (Ascomycota: Hypocreales: Clavicipitaceae), which systemically infect mostly grasses in the Poaceae, Juncaceae, and Cyperaceae (Clay, 1989; Breen, 1994). For example, *Neotyphodium*<sup>3</sup>-infected perennial ryegrass (*Lolium perenne*

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<sup>3</sup> Based on molecular analysis of 18S rDNA sequences, Glenn et al. (1996) created the genus *Neotyphodium* to include the following vertically transmitted endophytic anamorphs of *Epichloë* on C<sub>3</sub> grasses: *Acremonium coenophialum* Morgan-Jones & W. Gams, *A. typhinum* Morgan-Jones & W. Gams, *A. lolii* Latch, M.J. Chr. & Samuels, *A. chisosum* J.F. White & Morgan-Jones, *A. starrii* J.F. White & Morgan-Jones, *A. huerfanum* J.F. White, G.T. Cole & Morgan-Jones, *A. uncinatum* W. Gams, Petrini & D. Schmidt, and *A. chilensi* J.F. White & Morgan-Jones.

L.) and tall fescue (*Festuca arundinacea* Schreb.), have been shown to have negative effects on over 40 insect species in six orders (Clement et al., 1994). Variable effects have sometimes been reported, e.g. Clement et al. (2005) reported different effects on two aphids (bird-cherry oat aphid, *Rhopalosiphum padi* (L.) and rose grass aphid, *Metopopophium dirhodum* (Walker)) and the wheat stem sawfly (*Mayetiola destructor* (Say)) exposed to different wild barleys infected with *Neotyphodium*. Fewer studies have explored this relationship in nongrass systems. However, Jallow et al. (2004) reported drastic negative effects on larvae of *Helicoverpa armigera* Hübner reared on tomato plants infected with a nongrass endophyte, *Acremonium strictum* W. Gams.

Some endophytes belong to genera that include fungal entomopathogens such as *Beauveria* (Ascomycota: Hypocreales). *Beauveria bassiana* (Balsamo) Vuillemin has been reported as an endophyte in maize (Vakili, 1990; Bing and Lewis, 1991, 1992a,b; Lomer et al., 1997; Cherry et al., 1999, 2004; Wagner and Lewis, 2000; Arnold and Lewis, 2005), potato, cotton, cocklebur, and jimsonweed (Jones, 1994), tomato (Leckie, 2002; Ownley et al., 2004), on the cocoa relative *Theobroma gileri* (Evans et al., 2003), in the bark of *Carpinus caroliniana* Walter (Bills and Polishook, 1991), in seeds and needles of *Pinus monticola* Dougl. ex. D. Don (Ganley and Newcombe, 2005), in opium poppy (Quesada-Moraga et al., 2006), on date palm (Gómez-Vidal et al., 2006), in bananas (Akello et al., 2007), and in coffee (Posada et al., 2007, and this paper). In addition, cocoa (Posada and Vega, 2005) and coffee seedlings (Posada and Vega, 2006) have been successfully inoculated with *B. bassiana* by depositing a spore suspension on the radicle shortly after germination. Referring to *Beauveria globulifera* (= *B. bassiana*), Steinhaus (1949) wrote: “It also grows on corn and certain other plants but not so well as on insects.” No specifics were given on how these observations were obtained. Fuller-Schaefer et al. (2005) have reported on the colonization of sugarbeet roots by the fungal entomopathogens *B. bassiana* and *Metarhizium anisopliae* (Metschn.) Sorokin.

Other entomopathogenic fungi have also been reported as endophytes: *Verticillium* (= *Lecanicillium*) *lecanii* (Zimm.) Viégas in an Araceae (Petrini, 1981); *V. lecanii* and *Paecilomyces farinosus* (Holmsk.) Brown & Smith (= *Isaria farinosa*) in the bark of *C. caroliniana* (Bills and Polishook, 1991); *Paecilomyces* sp. in *Musa acuminata* (Cao et al., 2002) and in rice (Tian et al., 2004); and *Paecilomyces varioti* Bain. in mangroves (Ananda and Sridhar, 2002). *Cladosporium*, another genus containing insect pathogenic species (Abdel-Baky and Abdel-Salam, 2003 and references therein), has been reported as an endophyte in *Festuca* (An et al., 1993), in several Ericaceae (Okane et al., 1998), various grasses (Dugan and Lupien, 2002), mangroves (Suryanarayanan et al., 1998; Ananda and Sridhar, 2002), *Cuscuta reflexa* Roxb., *Abutilon indicum* (L.) Sweet and *Calotropis gigantea* (L.) R. Br. (Suryanarayanan et al., 2000), *M. acuminata* (Cao et al., 2002), wheat

(Larran et al., 2002a), oak (Gennaro et al., 2003), *Ilex* (Takeda et al., 2003), cacti (Suryanarayanan et al., 2005), and in apples (Cammatti-Sartori et al., 2005).

The negative effects of endophytic clavicipitalean fungi on insect herbivores have been generally ascribed to the production of fungal metabolites (Funk et al., 1983; Bush et al., 1997; Clay, 1988; Clay and Schardl, 2002), although environmental factors (Bultman and Bell, 2003) and presence of mycorrhizae and nutrients (Barker, 1987; Vicari et al., 2002) can influence the outcome of the association. The effects have also been shown to cascade to the third trophic level, e.g., parasitoids (Bultman et al., 1997). The effects of various nonclavicipitalean pine endophytes (e.g., *Phyllosticta*, *Rhabdocline*, *Leptostroma*, and *Cryptocline*) on spruce budworm (*Choristoneura fumiferana* (Clemens)) have also been ascribed to endophyte-produced metabolites (Clark et al., 1989; Miller et al., 2002).

The traditional mode of infection of fungal entomopathogens such as *B. bassiana* involves spore deposition on the insect cuticle followed by formation of a germ tube, which through enzymatic and mechanical action penetrates the cuticle (Hajek and St. Leger, 1994). Once in the hemocoel, hyphal growth causes tissue damage and nutrient depletion. Some entomopathogenic fungi are also known to produce metabolites (see Section 4) but their involvement in insect toxicosis is unclear (Gillespie and Claydon, 1989; Hajek and St. Leger, 1994).

The pioneering work on entomopathogenic endophytes was conducted using maize (*Zea mays* L.), *B. bassiana*, and the European corn borer, *Ostrinia nubilalis* (Hübner) as a model system. Season-long suppression of insects, measured as reduced tunneling of *O. nubilalis*, was achieved by applying *B. bassiana* in an aqueous (Lewis and Cossentine, 1986) or granular (Lewis and Bing, 1991) formulation on corn plants. Lewis and Bing (1991) suspected that *O. nubilalis* suppression was due to establishment of *B. bassiana* in the plant, based on prior reports of this phenomenon by Vakili (1990). In a subsequent paper, Bing and Lewis (1991) used granular formulations and injections of *B. bassiana* spore suspensions to obtain season-long suppression of *O. nubilalis* and concluded that this was due to *B. bassiana* becoming established as an endophyte in maize. Their methodology for assessing *B. bassiana* presence involved sterile techniques but does not report surface-sterilization (Bing and Lewis, 1991, 1992a), as is usually done when attempting to isolate endophytes (Arnold et al., 2001). Nevertheless, in a subsequent paper Bing and Lewis (1992b) report surface-sterilization of tissues and recovery of *B. bassiana*, thus providing evidence of an endophytic relationship. The possible mode of action for endophytic *B. bassiana* against *O. nubilalis* was not discussed in any of these studies or in subsequent studies (Lewis et al., 1996, 2001). The fact that no mycosed insects were reported (except for Bing and Lewis, 1993—see Section 4) suggests that the reduced tunneling reported in all the papers (Lewis and Cossentine, 1986; Lewis and Bing, 1991; Bing and Lewis, 1991; Bing and Lewis, 1992a,b;

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