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Mini-review

Fungus–plant interaction influences plant-feeding insects[☆]

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ABSTRACT

Fungal infection of plants alters plant metabolism and therefore their chemistry, by either increasing levels of defence compounds or decreasing levels of nutrients. Such alterations in plants, in turn, influence the performance of the insects that feed on them. Pathogenic fungi live on plants as either biotrophs or necrotrophs. Both bio- and necrotrophic fungi alter the physiologies of plants in distinctly different pathways. This article explores the patterns of relationships evident between insects and plants, the latter infected by biotrophic and necrotrophic fungi, using established examples from the vertically and horizontally transmitted biotrophic, endophytic fungi. A curious pattern evident in such interactions refers to the biotrophic, endophytic fungi that live in galls induced by the Cecidomyiidae (Diptera). The insects associated with necrotrophic fungi stand distinct from the patterns of interactions evident among insects, plants, and fungi. An understanding of the ecology of three-way interactions involving distantly related organisms, *viz.*, insects, fungi, and plants, will bear long-term consequences in the better management of annual crop and perennial forest trees. A majority of previously published papers in the context of insect–plant–fungus interactions liberally use the terms 'mutualism' and 'symbiosis', implicating the various benefits conferred on one or more of the participants. In the examples referred to, and the interacting contexts analyzed in this paper, what emerges is that the fungus is parasitically associated with the plant. In the eventuality of an insect interacting with the infected (= parasitized) plant, the insect gains (*e.g.*, gall-inducing Cecidomyiidae) or in occasional instances the plant gains (*e.g.*, *Epichloë* infections of Poaceae). A unifying model for insect–plant–fungus interacting systems is not readily apparent. The only possible explanation is the independent origins of insect behaviour in either preferring or rejecting the fungus-infected plants. This is possibly driven by specific environmental conditions, in which a specific fungus–plant–insect system would be operating.

1. Introduction

In nature, insects and plants associate in diverse ways. Plant-feeding insects depend on the nutrients provided by plants for their growth and reproduction, and use olfactory, chemoreceptory, and visual cues to either detect food or locate potential oviposition sites (Beyaert et al., 2010). Fungus-feeding insects, *e.g.*, the Attini (Hymenoptera), Erotylidae, Endomychidae, and Tenebrionidae (Coleoptera), are equally and remarkably divergent. The Macrotermitinae (Isoptera) are obligately mutualistic with *Termitomyces* (Lyophyllaceae). The Mycetophilidae and Phoridae (Diptera) use fungi during larval stages (Kerr, 2008). Mycophagy is known among the Tineidae (Lepidoptera), although the mechanisms of interactions remain unexplained (Hepener, 2008). Several Phlaeothripidae (Thysanoptera) feed on fungal mycelia, whereas the Idolothripinae feed on spores. The preference for a specific fungus varies with the species and this variability depends on diverse factors, including morphological features (*e.g.*, maxillary stylets), the degree of aggregation of food sources, and the abundance of fungi (Ananthakrishnan, 1993).

Pathogenic fungi are associated with plants either as biotrophs or as necrotrophs. Necrotrophs extract nutrients by killing host-plant tissues, whereas the biotrophs extract nutrients without doing so. Both induce specific, altered physiologies in their host plants. Plant-feeding insects and plant-pathogenic fungi often co-occur on the same plants (Karban et al., 1987). Many Hemiptera (*e.g.*, Aphidoidea, Jassoidea) transmit pathogenic microbes during

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[☆] This article celebrates the life and science of Chirayathumadom Venkitachalam Subramanian, a mycologist of repute and an authority of the Hyphomycetes.

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feeding. *Drosophila melanogaster* (Drosophilidae) mechanically disburses conidia of *Botrytis cinerea* (Sclerotiniaceae) (Louis et al., 1996). Some of these mechanical vectors can also transmit fungal spores both during feeding and through faecal material. Fungal infection of plants usually alters plant chemistry, by either increasing defence-chemical levels or decreasing the nutrient levels, which, in turn, can influence insect performance (Raman et al., 2012). Such changes affect the growth and development of insects negatively (Tasin et al., 2012). Low fecundity results in *Gastrophysa viridula* (Chrysomelidae) when feeding on the leaves of *Rumex crispus* and *Rumex obtusifolius* (Polygonaceae) infected by *Uromyces rumicis* (Pucciniaceae) (Hatcher et al., 1994). *Epirrita autumnata* (Geometridae) larvae experience detrimental effects during their life cycles, when feeding on *Betula pubescens* (Betulaceae) leaves infected with *Melampsoridium betulinum* (Pucciniastraceae) (Lappalainen et al., 1995). *Spodoptera frugiperda* (Noctuidae), when reared on *Lolium perenne* (Poaceae) infected with the asexual state of endophytic *Epichloë* (Clavicipitaceae), show reduced larval mass and delayed development compared with the larvae reared on uninfected *L. perenne* (Hardy et al., 1985). When infected by fungi (*e.g.*, *B. cinerea*, Sclerotiniaceae), *Vitis vinifera* (Vitaceae) leaves synthesize secondary metabolites, pathogenesis-related proteins, chitinase, and β−1,3−glucanase (Trotel-Aziz et al., 2006). In contrast, fungal infection can suppress plants' defence responses by altering secondary-metabolic pathways and improving nutritional quality, rendering the plant amenable for insect colonization (Cardoza et al., 2003). *Tischeria ekebladella* (Tischeriidae) larvae exhibit a better growth rate when they feed on leaves of *Quercus robur* (Fagaceae) infected by *Erysiphe alphitoides* (Erysiphaceae) (Tack et al., 2012). Improved survival and pupation rates of *Spodoptera exigua* (Noctuidae) occur when they feed on *Arachis hypogaea* (Fabaceae) foliage infected with *Sclerotium rolfsii* (Atheliaceae) (Cardoza et al., 2002).

Insects generally lack the capacity to synthesize sterols, which are the precursors for diverse hormones. Insects acquire either sterols or sterol precursors from plants and/or microbial symbionts (Svoboda and Weirich, 1995). The Psocoptera, Thysanoptera, Coleoptera, Diptera, Lepidoptera, Hymenoptera, and Isoptera derive the sterols that they require from fungi (Behmer and Nes, 2003). Plants usually include low levels of cholesterol, generally inadequate for insect development, yet the insects utilize available sterols. Sitosterol is one common plant sterol that supports insect growth and development. Stigmasterol, another common sterol usually occurring at much lower levels than the sitosterol (Akhisa and Kokke, 1991), is also utilized by insects. Most insects associated with fungi acquire ergosterol from fungi and metabolize it into cholesterol (Behmer and Nes, 2003). The Scolytinae (Coleoptera) feed on *Ambrosiella*, *Ceratocystiopsis* (Ceratocystidaceae), *Raffaelea* (Ophiostomataceae), and *Entomocorticum* (Basidiomycota) that grow as galleries within wood. The Scolytinae depend on ergosterol produced by associated fungi for successful oocyte development, oviposition, larval development, and pupation (Bentz and Six, 2006). *Dendroctonus ponderosae* (Coleoptera: Scolytidae) infesting *Pinus contorta* (Pinaceae) produce 20% more eggs when feeding on *Entomocorticum dendroctoni* (Basidiomycota) relative to other food sources (Whitney et al., 2011).

Pathogenic fungi modify plant-volatiles and their profiles (Witzgall et al., 2012). *Alternaria brassicae* (Pleosporaceae) infection of *Brassica rapa* (Brassicaceae) seedlings releases new volatiles arising from glucosinolate degradation (Doughty et al., 1996). Changes in plant odour are recognized by insects, which in turn, change their oviposition behaviour. *Lobesia botrana* shows a preference for berries of *V. vinifera* infected by either *Saccharomyces* (Saccharomycetaceae) or *B. cinerea* (Tasin et al., 2012). *D. melanogaster* also shows a significantly greater attraction towards *Saccharomyces cerevisiae*-infected berries of *V. vinifera* than the uninfected. In contrast, several plant-feeding insects avoid infected parts. *Hadena bicruris* (Noctuidae) avoids *Silene latifolia* (Caryophyllaceae) infected by *Microbotryum violaceum* (Microbotryaceae) (Biere and Honders, 1996) and *Phaedon cochleariae* (Chrysomelidae) avoids *A. brassicae* infected *B. rapa* leaves (Rostás and Hilker, 2002), possibly due to the volatiles produced by plants consequent to fungal infection.

Associations among vascular plants, fungi, and insects have a long history. The remains of *Psilophyton* (Trimerophytales) (Early Devonian, *c.* 400 mya) exhibit symptoms of damage caused by arthropods (extinct Hemiptera?) in addition to including fungal bodies in their cells (Banks and Colthart, 1993). Information on insect—fungus mutualism is available, which commenced with Joseph Schmidberger recognizing 'whitish' material that lined the tunnels made by *Apate terebrans* (= *Apate dispar*) (Bostrichidae) larvae in *Malus domestica* (Rosaceae) barks as ambrosia in 1836. Theodor Hartig in 1844 determined that this whitish material was a fungus. Subsequently, the term 'ambrosia beetles' came into use generically referring to the Scolytidea due to their intimacy with trees and fungi.

In view of the above complex and not well clarified kinds of interactions among the three distantly related genomes, we analyze the ecology of interactions among these organisms using representative examples. Most importarntly, we have grouped the interactions based on the nature of relationships between plants and fungi as either biotrophic or necrotrophic, since these appear more definitive. The physiological context of arthropods interacting with plants infected by biotrophic or necrotrophic fungi is the further layer added to this review. We think that an understanding of the ecology of such three-way interactions involving distantly related organisms bears long-term consequences in better crop management.

2. Biotrophic pathogenic and endophytic fungi and their influence on insects

Within the realm of biotrophic-fungal associations, we have delineated the vertically transmitted and horizontally transmitted fungi and how in such guilds the insects behave. Within the horizontal transmission pattern of biotrophic fungi associated with plants, another unique design becomes apparent especially among some of the gall-inducing insects.

2.1. Free-living insects and vertically transmitted endophytic fungi

Endophytic fungi associated with most plants are horizontally transmitted (Faeth and Fagan, 2002). However, those inhabiting above-ground tissues of Poaceae are generally transmitted vertically *via* seeds (Philipson and Christey, 1986), which are presently treated under *Epichloë* (Ascomycota) (Leuchtmann et al., 2014). Occasional explanations indicate that these fungi too are horizontally transmitted (Faeth et al., 2000). Less well studied for their effects on insects are *Epichloë*, which can manifest their sexual state externally on host plants. In *Epichloë*—Poaceae interactions, the stromata-bearing *Epichloë* bear negative consequences on Poaceae because of a parasitic association (Schardl et al., 2004). However, one species of *Botanophila* (Anthomyiidae) benefits from such a relationship (Bultman and Leuchtmann, 2008). Teleomorphic *Epichloë* association is explained as an evolutionary consequence which confers protection to Poaceae from insects because of the alkaloids produced by the fungus. This 'host-plant protection' proposal (Clement et al., 1994) is valid, since at least 40 insect species are influenced negatively by fungal alkaloids. Examples occur in improved *Lolium* (Poaceae) incorporated with *Epichloë*