



Mini-review

Fungus–plant interaction influences plant-feeding insects[☆]Anantanarayanan Raman^{a,*}, Trichur Subramanian Suryanarayanan^b^a Charles Sturt University and Graham Centre for Agricultural Innovation, P O Box 883, Orange, NSW 2800, Australia^b Vivekananda Institute of Tropical Mycology (VINSTROM), RKM Vidyapith, Chennai 600 004, India

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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.

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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 (Ananthkrishnan, 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

[☆] 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 disburse 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 *Melampsorium betulinum* (Pucciniaceae) (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 *Entomocorticium* (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 *Entomocorticium 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 importantly, 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) (Leuchtman 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 Leuchtman, 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*

(Clement et al., 2011). Defence against phytophagy varies depending on the interaction between specific insects and plants associated with specific fungi (Popay, 2009). Situations contradicting these also occur: e.g., *Festuca arizonica* (Poaceae) hosting *Neotyphodium starrii* indicates no anti-insect consequence (Faeth and Sullivan, 2003).

These interactions are generally mediated by alkaloids produced by the fungal associate within the host plant (Clay and Schardl, 2002). Peramine (a pyrrolopyrazine alkaloid) and ergot alkaloids are usually produced by the endophytic fungi associated with Poaceae. Lolitrems (indole-diterpenoid group) are produced by some strains of fungi that infect *L. perenne* (Popay et al., 1999). *L. perenne* infected by different strains of *Epichloë* (e.g., wild type, AR1, AR37) and those without the infection vary in their phenolic contents in the order '*L. perenne*+AR1' > '*L. perenne*+AR37' > '*L. perenne* (with no endophytic fungus)' > '*L. perenne* (wild type)' (Qawasmeh et al., 2012). Other indole-diterpenoids, such as epoxy-janthitrems are produced by '*L. perenne*+AR37' (Moore et al., 2015). Lolines are produced by '*Lolium arundinaceum*+*Epichloë coenophiala*' and '*Lolium pratense*+*Epichloë uncinata*'. Peramine deters *Listronotus bonariensis* (Curculionidae) adults, but has no effect on either *Heteronychus arator* (Scarabaeidae) (Ball et al., 1997) or *S. frugiperda* (Noctuidae) (Ball et al., 2006). Ergovaline deters *S. frugiperda* (Clay et al., 1989) and *H. arator* adults, and the larvae of *Popillia japonica* (Scarabaeidae) (Patterson et al., 1991) and *Agrotis ipsilon* (Noctuidae) (Potter et al., 2008). Lolitrem B influences (positively or negatively) growth and development of *L. bonariensis* larvae. Epoxy-janthitrems influence a range of insects, such as *L. bonariensis*, *H. arator*, *Balanococcus poae* (Pseudococcidae), *Wiseana cervinata* (Hepialidae), *Aploneura lentisci* (Aphididae), *S. frugiperda*, and *Chaetocnema pulicaria* (Chrysomelidae) (Raman et al., 2012), although the question whether the epoxy-janthitrems are solely responsible for the effect remains unanswered. Lolines are the most active known compounds that affect the life histories of insects, e.g., Aphidoidea (Wilkinson et al., 2000), *L. bonariensis* (Jensen et al., 2009), larvae of the Scarabaeidae (Popay and Lane, 2000), *S. frugiperda*, and *Ostrinia nubilalis* (Riedell et al., 1991). Variations in the strain of endophytic fungi impact *L. perenne*'s capacity to resist populations of *H. arator*. Volatile oils produced by different strains of endophytic fungi (e.g., wild type, AR37) in *L. perenne* enhance their resistance to insects. *L. perenne* (E⁻) produces 18 different volatile oils; the quantities of 2-ethyl-1-hexanol acetate, (Z)-2-octen-1-ol, and butylated hydroxyl toluene, however, were greater in *L. perenne* (E⁺) than those in *L. perenne* (E⁻) (Qawasmeh et al., 2014), wherein 'E⁺' refers to the Poaceae that would include the endophytic fungus and 'E⁻' refers to that devoid of the fungus.

In such associations, the fungus remains in leaf sheaths of tillers and never extends to roots (Moy et al., 2000). Maximal mycelial density occurs along stem bases and in actively growing axillary meristems. Concentrations of alkaloids, particularly ergovaline (Lane et al., 1997), lolitrem B (Ball et al., 1997), lolines (Justus et al., 1997), and epoxy-janthitrems (Tapper and Lane, 2004) are usually greatest in leaf sheaths and low in leaf blades. Seeds have high densities of mycelia and high-alkaloid concentrations. The distribution and concentration of alkaloids in Poaceae can influence insect behaviour and the responses of insects that feed on 'Poaceae (E⁺)'. Insects that feed either within or on leaf sheaths and at the meristematic region of the plant are often highly sensitive to fungi. *L. bonariensis*, species of *Sphenophorus* (Dryophthoridae), *H. arator*, and *B. poae* feed on these plant parts and are highly responsive to fungal incidence. The survival of *Rhopalosiphum padi* (Aphididae) is compromised if it would occur only in leaf sheaths of *L. arundinaceum* (E⁺), but it survives better feeding on leaf blades (Hunt and Newman, 2005). Similarly, feeding by *Parapediasia teterrella* (Crambidae) on leaf sheaths of '*L. perenne*+*Neotyphodium*

lolii' alters its life-history performance (Kanda et al., 1994). Endophytic-fungal infection also alters the distribution of *Blissus* (a species of Lygaeidae) on North-American plants, whose preferred habitats are leaf sheaths and crowns (Mathias et al., 1990). However, *S. frugiperda* feeding on leaf blades show varied responses, from negative (mortality) to positive (better growth and development) (Ball et al., 2006). The Aphididae and Cicadellidae also exhibit varied responses to endophytic-fungal infection depending on the insect species and plant—fungus association. Populations of root-feeding *A. lentisci* (Hemiptera: Aphididae) decline markedly due to endophytic fungi in *L. arundinaceum*, *L. pratense*, and *L. perenne* (Popay and Gerard, 2007). Movement of alkaloids away from the location of the alkaloid-producing fungus probably results in their greater concentrations in vascular than cortical tissues. Such a movement has strong effects on the Hemiptera, but more variable effects on root-chewing larvae of the Scarabaeidae (Coleoptera). Populations of '*L. arundinaceum* (E⁺)' and '*L. pratense* (E⁺)' produce loline alkaloids affecting the survival and growth of Scarabaeidae larvae (Koppenhofer and Fuzy, 2003).

'*L. pratensis*+*E. uncinata*' contains high concentrations of lolines which retards growth of the larvae of *Costelytra zealandica* (Scarabaeidae). Feeding on roots by *C. zealandica* induces the redistribution of lolines, thus resulting in high concentrations in roots (Patchett et al., 2008). Different strains of *Epichloë* are responsible for the production of specific alkaloids, but the host-plant genotype can also modify expression of alkaloids *in situ* (Qawasmeh et al., 2011). Endophytic-fungal infection can alter the biosynthesis of both primary and secondary metabolites, changing the plant's nutritional quality and consequently, its attractiveness to insects (Rasmussen et al., 2007, 2008a, b). The density of fungal infections in plants, climatic factors affecting their density, concentrations of metabolites, and plant nutrition contribute to insect deterrence (Miranda et al., 2011). *R. padi* (Aphididae) is negatively affected by drought stress, but only when feeding on endophytic fungus-free plants; in contrast, the larvae of *S. frugiperda* perform poorly on drought-stressed, endophyte-infected plants (Bultman and Bell, 2003). *R. padi* reproduces quickly on regenerating tissue of uninfected plants, but endophytic-fungal infection nullifies that outcome. In contrast, the larvae of *S. frugiperda* are unaffected during interactions between damage and infection. Importantly, *E. coenophiala* does not provide universal deterrence against insects (Bultman and Bell, 2003). Endophyte-mediated deterrence varies with insect species and will be a complex function of stress driven by environmental factors such as drought. The Poaceae (E⁺) deter insects through innate resistance mechanisms such as antixenosis. Therefore, the effects of endophytic fungi on insects will depend on a balance between those factors that stimulate the insect to feed and those that deter it. The deterrence to endophytic fungi in many insects may have evolved as a mechanism to avoid negative effects of other allelochemicals that the fungus produces. Adult deterrence results in reduced oviposition as evident in *L. bonariensis* (Barker et al., 1984) and *H. arator* (Prestidge and Ball, 1993) that may protect the offspring from exposure to negative effects (Popay, 2009). In field conditions, populations of insects that are adversely affected by endophytic fungal infection are low on grasses whenever a high frequency of infection occurs (Raman et al., 2012).

Endophytic-fungal infection of Poaceae has implications at other trophic levels. For instance, responses of insect parasitoids to arthropod hosts are influenced by Poaceae (E⁺) (Bultman et al., 2009, 2012). The activity of Lycosidae (Arachnida) was significantly greater on infected *L. perenne* in warmer seasons, when populations of prey insects (e.g., Aphididae, lepidopteran larvae, and dipteran larvae) were similar in the pastures that included both '*L. perenne* (E⁺)' and '*L. perenne* (E⁻)' (Prestidge and Marshall, 1997). Endophytic-fungal infection of *L. perenne* reduced the

attractiveness of *A. ipsilon* (Noctuidae) to entomophagous *Steinernema carpocapsae* (Nematoda: Steinernematidae) (Kunkel and Grewal, 2004). This reduced susceptibility to *S. carpocapsae* when its host insects were feeding on 'Poaceae (E+)' has been attributed to direct effects of alkaloids of endophytic origin on *Xenorhabdus nematophila* (Enterobacteriaceae) that are symbiotic with *S. carpocapsae* (Richmond and Bigelow, 2009). In contrast, the larvae of *P. japonica* (Scarabaeidae) feeding on infected *L. arundinaceum* and *Lolium rubra* subsp. *falax* were more susceptible to infection by *Heterorhabditis bacteriophora* (Nematoda: Heterorhabditidae) (Grewal et al., 1995).

2.2. Free-living insects and horizontally transmitted endophytic fungi

Fungi form localized infections in angiosperms, gymnosperms, pteridophytes, bryophytes, and macroalgae, and are transmitted horizontally (Arnold and Lutzoni, 2007). Although these fungi occur ubiquitously, they have been explored principally for their ability to elaborate novel bioactive metabolites and manipulate those of their host plants (Suryanarayanan et al., 2009). Some of these endophytes produce compounds such as paclitaxel, camptothecin, podophyllotoxin, deoxypodophyllotoxin, hypericin, and emodin (Kusari and Spiteller, 2012), although their exact role in either attracting or deterring insects is not clearly established.

With a wide range of fungi occurring endophytically in nearly all of the plant kingdom, a staggering variety of interactions involving plants, fungi, and insects is apparent (Suryanarayanan, 2013). For instance, the density of endophyte fungi, and not the diversity, was lower in *Bacillus thuringiensis* (Bt) gene-incorporated varieties of *Gossypium hirsutum* (Malvaceae) than the non-Bt included varieties, indicating that the insects visiting *G. hirsutum*, for either pollination or feeding are directly related to the density of fungal infection; it is possible that the associated insects carry the fungal inoculum and infect the plant while feeding on *Gossypium* (Suryanarayanan et al., 2011). *Atta colombica* (Formicidae), a defoliator of various Neotropical plants, prefers leaves with low-endophyte density thus possibly minimizing plant's energy expenditure for including the fungi (van Bael et al., 2009). Circumstantial evidence suggests that the insect faeces serves as a substrate for the fungi to grow and sporulate, increasing their inoculum load in the environment (Frost and Hunter, 2007). *Glomerella cingulata* (Glomerellaceae) occurring as an endophyte in the leaves of *Calotropis gigantea* (Apocynaceae) transits through the digestive tract of *Poeciloceris pictus* (Pyrgomorphidae) and sporulates on the frass (Devarajan and Suryanarayanan, 2006). The mechanism of stress tolerance induced by endophytic fungi in plants in the overarching context of insect feeding is not yet well clarified. Generally, plants with endophytic fungi deter insect feeding (Mejía et al., 2008; van Bael et al., 2009). One potential explanation is that fungal infection leads to an upscaling of defence genes involved in the ethylene pathway and activating receptor kinases in plants, thus enabling them to resist insects (Mejía et al., 2014). A recent study on the root endophyte *Piriformospora indica* indicates that the fungus could increase the resistance of *Oryza sativa* roots to *Lissorhoptrus oryzophilus*, via modifications in gibberellin- and jasmonate-signal pathways (Cosme et al., 2016).

Metarhizium robertsii (Clavicipitaceae), an entomopathogenic fungus generally from soil, builds an organic connection with roots of *Phaseolus vulgaris* (Fabaceae) and *Panicum virgatum* (Poaceae). This soil fungus colonizes host tissues as an endophyte and transmits nitrogen from the insects to the plant (Behie and Bidochka, 2014). If this phenomenon is more common, it could be envisaged that such fungal endophyte—plant mutualisms would enable better stress tolerance in plants, bearing a critical influence on the

next-level consumer organisms, viz., insects. Behie et al. (2017) have shown that the endophytic capability and insect pathogenicity of *M. robertsii* enables exchange of insect-derived nitrogen with the plant's photosynthate to the fungus. By using ^{13}C , they have shown the incorporation of ^{13}C into photosynthate and the subsequent translocation of ^{13}C into fungal-specific carbohydrates (trehalose and chitin) in the root—endophyte complex.

Another novelty in such three-way interactions is the capacity of other entomopathogenic fungi such as *Beauveria bassiana* (Cordycipitaceae) to grow endophytically in the above- and below-ground plant tissues (Vidal and Jaber, 2015). *B. bassiana* grows as a horizontally transmitted endophyte in *Zea mays* (Poaceae) causing high mortality of *O. nubilalis* (Lepidoptera: Crambidae) larvae when they feed on *Z. mays*+*B. bassiana* (Bing and Lewis, 1991). With the possibility of using endophytically functioning entomopathogenic fungi as agents in the biological management of insect pests, studies on endophytic—entomopathogenic fungi have intensified. *Metarhizium anisopliae* and *Lecanicillium lecanii* (Clavicipitaceae) live endophytically in various plants. *Coffea arabica* (Rubiaceae) in Hawaii, Colombia, Mexico, and Puerto Rico harbour species of *Acremonium*, *Beauveria*, *Cladosporium*, *Clonostachys*, and *Paecilomyces* as endophytes (Vega et al., 2008). Entomopathogenic fungi living as endophytes are conceptually attractive for potential management of arthropod pests. Whereas *B. bassiana* can live endophytically in both dicotyledonous and monocotyledonous plants, the host range of other entomopathogenic, endophytic fungi is not yet defined (Vidal and Jaber, 2015). Moreover, for the successful implementation of endophyte-mediated biological management of insect pests, an effective entomopathogenic endophytic fungus should be checked for the absence of mycotoxin production as well as for its ability to colonize and grow systemically in a crop overcoming competition and antagonism of native endophytic organisms (Suryanarayanan et al., 2016).

2.3. Gall-inducing insects and horizontally transmitted endophytic fungi

Many Thysanoptera, Hemiptera, Diptera, Lepidoptera, Coleoptera, and Hymenoptera induce galls on plants. Their larvae feed and live within galls (Raman, 2011). Fungi associate with gall-inducing insects in multiple ways. Many are saprotrophs (Raman, 1987), whereas a few others function as either parasites or pathogens (Butin, 1992). Some, known as the ambrosia fungi (Meyer, 1952), occur in galls induced by specific tribes of the Cecidomyiidae (Diptera) by associating themselves symbiotically with the insect, whereas in galls induced by the Hymenoptera (e.g., Cynipidae) and Hemiptera (e.g., Aphidoidea, Psylloidea) the fungi do not operate so intimately.

Specific Asphondyliini, Alycaulini, and Lasiopterini (Cecidomyiidae) induce 'ambrosia' galls (Yukawa and Rohfritsch, 2005). Such galls include no well-defined nutritive tissue (*sensu* Bronner, 1992). Instead, they include fungal mycelia lining the inner perimeters of larval chambers, providing nutrition for the developing larva (Neger, 1908, 1910; Richter-Vollert, 1964; Rohfritsch, 2012). The fungus usually occurs in galls from the time of occupation by the neonate larva. The fungus proliferates and fills up the larval chamber once the larva is either killed deliberately or dies naturally. High RNA concentration and acid-phosphatase activity in the mycelia that line the inner walls of galls reinforce that the fungus nourishes the larvae (Bronner, 1977). These Cecidomyiidae that induce ambrosia galls display features reminiscent of the ancestral mycetophagous habit: the intestines in their larvae are similar to those of fungus-feeding Cecidomyiinae (Roskam, 1992, 2005). The mechanisms of introduction of the fungal inoculum vary. In the Asphondyliini, the gravid female uses her pointed ovipositor to

insert eggs with fungal inoculum into the plant. In the Alycaulini and Lasiopterini, neonate larvae introduce the fungus into the plant tissue during feeding (Yukawa and Rohfritsch, 2005). *Meria parkeri* (Hemiphacidiaceae) occurs in galls induced by *Contarinia* (Cecidomyiidae) on *Pseudotsuga menziesii* (Pinaceae). These galls also include the teleomorph *Rhabdocline parkeri*. Larval mortality is high in galls that include *R. parkeri* (Carroll, 1986). The presence and performance of gall-inducing Cecidomyiidae are influenced by either the presence or the absence of endophytic fungi (Gagné, 1996).

In galls induced by *Daphnephila* (Cecidomyiidae) on *Machilus thunbergii* (Lauraceae) in Northern Taiwan, the larvae use *Botryosphaeria dothidea* (Botryosphaerales: Botryosphaeriaceae) to activate plant cells and to extract nourishment (Pan et al., 2015). However, other fungal species also co-exist in *Daphnephila* galls (e.g., species of *Fusarium*, Hypocreales: Nectriaceae; species of *Pestalotiopsis*, Xylariales: Amphisphaeriaceae). The other fungi isolated from *M. thunbergii* galls possibly play a role in the better nourishment of *Daphnephila*, which remains to be established. This pattern, i.e., a community of one principal, specific fungus and multiple nonspecific fungi, appears as a common feature in galls induced by the Asphondyliini (Tokuda and Yukawa, 2007). The current explanation is that the taxa belonging to advanced Tribes of the Cecidomyiidae remain specific to specific fungi, whereas those belonging to primitive Tribes of the Cecidomyiidae are associated with multiple fungi, some saprotrophic and others biotrophic. Galls induced by *Daphnephila* of the Asphondyliini Tribe include more than one fungal taxon. *Daphnephila* bears a nonsclerotized, blunt-tipped ovipositor (Tokuda et al., 2008), but whether the blunt tip of the ovipositor has a role in picking up and dispersing multiple fungal taxa remains a question.

Cynipidae (Hymenoptera) that induce galls on *Quercus garryana* (Fagaceae) suffer almost 100% mortality when the galls are artificially injected with spore suspensions of an endophytic fungus (Wilson, 1995). Similarly, *Contarinia* (Cecidomyiidae) larvae on *P. menziesii* show high mortality when sprayed with spores of *R. parkeri* (Carroll, 1991). Endophytic *Cladosporium* (Cladosporiaceae) in galls on *Quercus agrifolia* (Fagaceae) influence the mortality of gall-inducing *Dryocosmus dubiosus* (Cynipidae) (Taper and Case, 1987). Endophytic *Discula quercina* (Gnomoniaceae) causes mortality of *Besbicus mirabilis* (Cynipidae) but not *Bassetia ligni* (Cynipidae) when both induce galls on *Q. garryana* (Wilson, 1995). *B. mirabilis* prefers to occupy the part of the leaf where endophyte infection is low. Populations of *B. ligni* spatially correlate within leaves with the presence of the endophytic fungus, but suffer no fungus-induced mortality. However, *B. ligni* occupies the leaf lamina, where the fungus shows no growth, in contrast to the leaf midrib, where *B. mirabilis* galls occur. Further, *B. ligni* emerge from galls when fungi are most abundant, so this species temporally avoids prolonged contact with the infected tissue. However, the between-leaf distributions of both insects were independent of endophyte infection (Wilson and Carroll, 1997).

Little is known regarding fungi and their role in galls of Hemiptera. *Cladosporium sphaerospermum* (Cladosporiaceae) in galls on *Picea glauca* (Pinaceae) causes mortality of gall-inducing *Adelges abietis* (Adelgidae) (Lasota et al., 1983). Fungi in galls induced by *Pemphigus betae* (Eriosomatinae) on *Populus angustifolia* (Salicaceae) function as inquilines initially. With time *P. betae* populations in galls die since the fungus turns necrotrophic, killing tissues of *P. angustifolia* (Wilson, 1995).

3. Necrotrophic fungi and their influence on insects

Necrotrophic fungi associated with plants are pathogenic, but the physiology of their disease induction is not as extensively

explained as with the biotrophic fungi. Necrotrophic fungi (e.g., *B. cinerea*) secrete cell-wall degrading enzymes such as polygalacturonases (Prins et al., 2000) to lyse host cell walls and the oligosaccharides released in consequence regulate insect perception and response signals (Malinovsky et al., 2014). They also synthesize pectinolytic and cellulolytic enzymes to separate infected cells within hosts, which consequently release volatiles, such as 3-methyl-1-butanol and phenethyl alcohol from host plants (Rizvi and Raman, 2016a).

Fungi-induced volatiles from plants influence the behavioural dynamics of insects. Leaves of *A. hypogaea* infected by *S. rolfsii* release *E*-4,8-dimethyl-1,3,7-nonatriene, (*E,E*)-4,8,12-trimethyl-1,3,7,11-trideca-tetraene, methyl salicylate, and 3-octanone, which function as attractants for *S. exigua* (Noctuidae) (Cardoza et al., 2002). *B. cinerea* infection of *V. vinifera* leaves releases lipoygenase-inhibiting compounds, e.g., hexanal, 1-hexanol, 2-hexen-1-ol (*E*), (*E*)-3-hexen-1-ol, 1-octen-3-ol, which alter *Epiphyas postvittana*'s oviposition behaviour (Rizvi et al., 2014, 2015). The level of infection of *V. vinifera* by *B. cinerea* regulates the intensity of production of other secondary metabolites such as alcohols, ketones, aldehydes, aromatic hydrocarbons, and terpenes, which, in turn, influence the Lepidoptera—*V. vinifera* interactions (Tasin et al., 2012). Gravid females of *E. postvittana* avoid *B. cinerea*-infected *V. vinifera* leaves for oviposition and the rate of oviposition is inversely related to the intensity of infection (Rizvi and Raman, 2015a). A necrotrophic fungus-infected plant could be a source of food for the Lepidoptera (Cardoza et al., 2003; Rizvi and Raman, 2015b). However, the time difference between oviposition and egg hatch increases with levels of infection and consequently the potential larval food could deteriorate in quality (Tasin et al., 2012).

E. postvittana larvae carry viable conidia of *B. cinerea* both externally and internally, transmitting conidia to uninfected sites on *V. vinifera* by either shedding them on hosts or via faeces. When experimentally forced to live on intensely infected leaves of *V. vinifera*, *E. postvittana* larvae die before pupation. In contrast, feeding on mildly infected leaves improves their performance. In such a context, their avoidance of intensely infected leaves of *V. vinifera* impresses as an adaptive strategy, ensuring a better survival. In response to *B. cinerea* infection, *V. vinifera* leaves synthesize new enzymes such as chitinase and β -1,3-glucanase, which could function as anti-insect compounds (Vihervuori et al., 2013). Production of these compounds by *V. vinifera* in response to *B. cinerea* infection could be one reason for *E. postvittana* larval mortality. Curiously *B. cinerea* infection of berries of *V. vinifera* does not inhibit attraction of *E. postvittana* larvae. With berries ripening, some of the defence compounds either do not manifest or are modified into non-defence compounds (Jeandet et al., 1995). Fungal infection can decompose complex organic material into simpler forms (Cardoza et al., 2003) explaining why *E. postvittana* larvae show a better life-history performance while feeding on *B. cinerea*-infected *V. vinifera* (Rizvi and Raman, 2016b).

The quality and quantity of deterring compounds determine the range and use of plants by many polyphagous insects (Suckling and Brockerhoff, 2010). *E. postvittana* larvae do not show any preference between diets with or without Bt endotoxins at the beginning. However, over time the larvae prefer diets without the endotoxins (Harris et al., 1997). These indicate that gustatory cues influence *E. postvittana*'s decision to either progress with feeding or not (Harris et al., 1999). *E. postvittana* larvae show no significant preference for artificial diets incorporated with lyophilized mycelia of *B. cinerea* over the artificial diet without the fungus material (Rizvi and Raman, 2015a), although artificial diet incorporated with lyophilized mycelium improves the life-history performance of the larvae.

The degree of fungal infection influences mutualistic relationships between plants and insects (Biere and Tack, 2013). Low-infection levels of *Pinus radiata* (Pinaceae) by *Ophiostoma ips* (Ophiostomataceae) enables adults of *Ips pini* (Curculionidae) to colonize the sapwood of *P. radiata*, but a high degree of infection detrimentally affects development of *I. pini* larvae (Kopper et al., 2004). A similar outcome has been observed in *in vitro* experiments with *E. postvittana*—*V. vinifera*—*B. cinerea* (Rizvi and Raman, 2015a). Mild to modest infection levels generally enhance *E. postvittana* nutrition and result in better life-history performance, but this is not true at high degrees of infection. The latter could be because the complex nutrient materials are broken down into simpler forms and/or levels of defence compounds decrease. Sublethal infections of *Athelia rolfsii* (Atheliales: Atheliaceae) on *A. hypogaea* had a limited effect on *S. exigua* larvae, whereas a high intensity of *A. rolfsii* reversed that effect (Cardoza et al., 2003). However the caveat remains that an infection can deteriorate potential food quality and enhance toxicity (Tasin et al., 2011). Fungal infection can lower nitrogen levels in plant tissues (Hatcher, 1995). That the carbohydrate—nitrogen ratio regulates insect development is obvious in *Choristoneura occidentalis* larvae (Tortricidae) suffering deleterious growth when fed on high carbohydrate—low nitrogen food (Clancy, 1992). Detrimental effects on the life-history performance of *G. viridula* have been related to low-nitrogen levels of *U. rumicis*-infected *Rumex* leaves (Hatcher et al., 1994). *B. cinerea* kills plant cells with various sesquiterpenoids (e.g., botrydial, botrydial, 8, 9-epibotrydial) (Hof and Kupfahl, 2009). Insects differ in their capacities to breakdown such compounds. For example, *S. frugiperda* larvae can detoxify trichothecenes such as 4-monoacetoxyscirpenol (a mycotoxin produced by *Fusarium roseum*, *Fusarium sulphureum*, Hypocreales: Nectriaceae) more effectively than those of *Helicoverpa zea* (Lepidoptera: Noctuidae) (Dowd and van Middlesworth, 1989). Occasionally, the compounds of fungal origin can synergize with allelochemicals — that can be toxic to the consumers — produced by plants (Hatcher, 1995): fusaric acid can synergize with allelochemicals of *G. hirsutum*, such as gossypol and the synergized compound increases the mortality and decreases the development rate of larvae of *H. zea* (Vining, 1990).

Many insects have developed the capacity to feed on fungal mycelia and spores, which include sterol sources. *Hypothenemus hampei* (Coleoptera: Curculionidae) feed on *C. arabica* (Rubiaceae) berries, but can neither moult nor reproduce without the ergosterol obtained from *Fusarium solani* in the host plant (Morales-Ramos et al., 2000). Mature berries of *V. vinifera* are the least preferred by *E. postvittana* larvae, since sterol levels in berries drop significantly with maturation (Le Fur et al., 1994). The reliance of *E. postvittana* on *B. cinerea* clarifies the vitality of sterols and vitamins from fungi necessary for larval metamorphosis (Mondy and Corio-Costet, 2000). Fungal infection often changes the quality of infected tissues (Farrar and Lewis, 1987). For example, when insects feed on *Lolium multiflorum* foliage infected by *Drechslera siccans* (Pleosporales: Pleosporaceae), the insects consume greater quantities of either plant allelochemicals or fungal compounds, which can affect their development rate negatively and increase their mortality rate (Slansky and Wheeler, 1992).

Some insects feed on fungi with no explicit demonstration of a specialized relationship such as mutualism. *Sirex noctilio* (Siricidae) larvae are obligate symbionts with *Amylostereum areolatum* (Amylostereaceae) and only survive in *A. areolatum*-infected *P. radiata* (Pinaceae) (Slippers et al., 2003). Tortricidae larvae show a better life-history performance when feeding on diets incorporating *B. cinerea* mycelial material (Rizvi et al., 2015). Reproduction in several insects is closely linked to feeding patterns of insects evident during their larval phases. For instance oocyte production (in adults) depends on the quality of food consumed by them

during their larval periods since the bulk of nitrogen and carbon components of eggs is derived from nutrients obtained during the larval period. *B. cinerea* amended diet significantly enhances fecundity and fertility of *E. postvittana*. Similar results have been observed for *L. botrana* larvae fed on artificial diet incorporating mycelium (Tasin et al., 2011) or purified sterols of *B. cinerea* (Mondy and Corio-Costet, 2000). Also, *Aphis fabae* (Aphididae) develops more rapidly, attains a heavier pupal mass, and lays more eggs when fed on *Botrytis fabae* (Helotiales: Sclerotiniaceae)-infected *Vicia faba* (Fabaceae) (Zebitz and Kehlenbeck, 1991). Similarly, larvae of *Apion onopordi* (Apionidae) that developed on *Puccinia punctiformis* (Pucciniaceae)-infected *Cirsium arvense* (Asteraceae) lay almost twice as many eggs than those feeding on uninfected *C. arvense*.

4. Synthesis

Plant responses to fungi and insects vary widely. In this article, we have considered the plant-pathogenic fungi as biotrophs and necrotrophs and how such associations are tackled by insects. The fungi operating in strongly varying guilds induce specific physiological responses in plants, and consequently on insects associated with them. With the available information, developing a general statement on the biology and behaviour of biotrophic endophytic fungi is not only difficult, but also perplexing. When associated with Poaceae these fungi enable plants with a capacity to deter insects. Systemic, vertically transmitted endophytic fungi (e.g., *Epichloë*) play a greater role in strengthening plants more than the nonsystemic, horizontally transmitted fungal endophytic fungi, such as *Colletotrichum* (Glomerellaceae) and *Sphaeropsis* (Ascomycota). On the contrary, when associated with plants in the context of galls, the biotrophic fungi serve as the source of nutrition for the Cecidomyiidae.

Horizontal transmission and high diversity in forms (recognized as anamorphs) when the fungi occur endophytically in plants reinforce antagonistic interactions between fungi and plants (Leigh, 1999). High incidence of endophytic fungi among unrelated plants indicates inconsistent infection styles by particular fungal taxa (Arnold et al., 2003). This level of inconsistency in infection styles is highly unlikely to play any significant defence role in the plants they infect (Faeth and Sullivan, 2003). In addition, localized infections by horizontally transmitted fungi (referred to as the 'endophyte space') are generally avoided by insects, whereas such behaviour is not apparent among the insects that attack Poaceae with vertically transmitted systemic infections. The secondary metabolites that arise in the vertically transmitted *Epichloë*—Poaceae associations seem to provide a comprehensive defence package in plants. Nevertheless, further studies on the production and effects of secondary metabolites (e.g., alkaloids) by horizontally transmitted fungi may provide more evidence and their function in 'protecting' plant tissues. Some evidence prevails that the horizontally transmitted endophytic fungi have a capacity to defend plants from insects, although such defences are unlikely to be robust and as apparent as in obligate biotrophic endophytic fungi interacting with Poaceae. A high level of diversity occurs in *Epichloë*—Poaceae relationship and their role in the defence of plants from insects stands reasonably well clarified. One practical gain of such an understanding of this biology is that it has led to the breeding of 'improved' pasture taxa, such as *L. perenne* and *L. arundinaceum*, integrating the genetic material of endophytic fungal strains. Integrating *Epichloë* genetic material into Poaceae for use in grazing systems creates an artificial association between the two. What we need to recognize here is that the expression of alkaloid production capacity — presently perceived as an advantage in production systems — can change over time and in

succeeding generations (Qawasmeh et al., 2011). Artificiality in breeding exercises, invoking the breaking of natural barriers by human intelligence, often has negative consequences, such as the possible reversal to parental traits in the offspring over time. The physiology of the ‘newly created’ individuals often influences developmental and behavioural traits in plants (Cheverud and Moore, 1994).

In the context of biotrophic endophytic fungi in Cecidomyiidae-induced galls, the larva utilizes the fungus as a food source; in instances of fungal occurrence in Cynipidae-induced galls, the fungus functions as a defence against unfavourable organisms, somewhat similar to the *Epichloë*–Poaceae interactions, and not as a source of nutrition for the inhabiting Cynipidae (Kobune et al., 2011). Fungal associates possibly enable plant exploitation by the Cecidomyiidae, which are usually selective of plants (Raman, 1996). The generally pathogenic *B. dothidea* (Janson et al., 2008), when associated with Cecidomyiidae-induced galls do not behave as pathogens. *Asteromyia carbonifera* (Cecidomyiidae) induces galls on c. 60 species of *Solidago* in North America (Gagné, 1989), all of which include *B. dothidea* (Heath and Stireman, 2010). Such contexts of association of *B. dothidea* in galls induced by the Cecidomyiidae is similar to the functions of subcellular microbial mutualists (e.g., ‘endomycorrhiza’, *Buchnera* [Enterobacteriaceae] in the guts of various Hemiptera) possibly due to the evolutionary success of their pathogenic precursors that have enabled them to exploit plants. Such a fungal association with the Cecidomyiidae-induced galls is also being interpreted differently (Joy, 2013, p. 1): “Symbiotic lineages (*sic.* of the Cecidomyiidae) have undergone a manifold expansion in the range of host-plant taxa they use relative to lineages without such fungal symbionts, as defined by the genetic distance between host plants. Furthermore, symbiotic gall-inducing insects are many more times as diverse as their non-symbiotic relatives.” Symbiotic interaction leads to niche expansion, according to Joy (2013), which in turn catalyzes diversification; in such a context the fungi seem to play a unique and a distinctly different role.

Necrotrophic fungi alter host-plant metabolism mainly by killing host tissues. Such killing bears significant effects on the population dynamics and life-history performance of associated insects (Stout et al., 2006; Biere and Tack, 2013). *O. nubilalis* (Crambidae) larvae develop nearly 20% faster on *Z. mays* (Poaceae) tissues infected by *Glomerella graminicola* (Glomerellaceae) than those living on uninfected *Z. mays* (Carruthers et al., 1986). *A. onopordi* (Apionidae) show higher survival rate and better life-history performance, while feeding on *P. punctiformis* infected shoots of *C. arvensis* than on uninfected shoots (Bacher et al., 2002). In contrast, infection of *C. arvensis* by *Phoma destructiva* (Pleosporales) reduces oviposition, feeding, survival and growth rates, and pupal mass of *Cassida rubiginosa* (Chrysomelidae) (Kruess, 2002). Similar reduction in the life-history performance of *Melitaea cinxia* (Nymphalidae) larvae feeding on *Plantago lanceolata* (Plantaginaceae) infected by *Podosphaera plantaginis* (Erysiphaceae) is known (Laine, 2004). Avoidance of a diseased plant, especially those infected by necrotrophic fungi could be an adaptive strategy among insects. Although the infected plants, sometimes, provide readily available food to the developing larvae, by breaking complex materials into simple forms, intensifying infections by necrotrophic fungi can deteriorate the quality of food. For instance, gravid *E. postvittana* does not lay eggs on infected sites of either leaves or berries, although eggs occur close to infected sites (Rizvi et al., 2015; Rizvi and Raman, 2015a). *E. postvittana* larvae can complete their life stages feeding solely on *V. vinifera* leaves (Rizvi and Raman, 2015a). Larvae of the same *E. postvittana* experience detrimental effects on development and reproductive potential when fed on uninfected, healthy berries, compared with those fed on *B. cinerea*-infected berries (Rizvi et al., 2015). Lack of sterols in

the berries could be one reason for that detrimental effect on *E. postvittana*. *B. cinerea* infection on berries potentially supplements the ‘necessary’ sterols to the developing larvae of *E. postvittana*. *B. cinerea*-infected berries of *V. vinifera* significantly improved larval and adult performance of *E. postvittana* (Rizvi et al., 2015), apparently supplying the required nutrients to the larvae.

5. Conclusion

Interactions between insects and plants have been explored intensely and convincingly in the last few decades; many books, research articles, and reviews refer to them plentifully. The involvement of a fungus in the interaction between a plant and an insect make the interaction more complex and dynamic, however, only in the recent past have we started examining the three-way interactions among these participants. In such a context, we featured the fungus as biotrophs and necrotrophs. We are not sure whether such a categorization of fungi based on their functional status is the most appropriate way to understand the tripartite interaction. We recognize that interacting elements in nature change their behaviours over extremely long or short time frames. Learning behaviour in insects particularly imposes alterations in them, which are encoded in their germplasm in the long term; the plants alter their response behaviours similarly (Webster and Cardé, 2016), although several other variables — both biotic and abiotic — play a role in this complex set of interactions. In such a background, we have narrowed our scope in this review to the role and effects of an extraneous element, *viz.*, fungus, in influencing plant-feeding insects. We are currently at a position to demonstrate that the fungi induce alterations in plants which in turn modify the volatiles arising from plants, which in turn influence the insect, either as an attractant or as a deterrent. Previous literature referring to insect—plant—fungus interactions uses ‘mutualism’ and ‘symbiosis’ implying the ‘advantages’ conferred in consequence to one or more of the participants. In the contexts analyzed and explained above, what emerges is that the fungus derives its nutrition from the plant, and hence, in principle, a parasite. When an insect interacting with the infected (parasitized) plant, is negatively affected, this would benefit the plant and so the endophytes would be considered a mutualist. This would certainly not be the case if the insect benefits from the incidence of the fungal endophyte, as evident in the behaviour of gall-inducing Cecidomyiidae.

This review focuses on the behaviour of herbivorous insects while feeding on plants infected by biotrophic and necrotrophic fungi. Some patterns are apparent when interactions between plants and fungi alone are considered. However, when we add the next layer of organisms, *viz.*, herbivorous insects into this context, no obvious pattern is discernible. The only possible explanation is the independent origin of insect behaviour, while either preferring or rejecting fungi-infected plants. This could possibly be driven by specific environmental conditions, in which a specific fungus—plant—insect system would be operating. Various species of biotrophic fungi are associated with galls induced by the same species of Cecidomyiidae. Use of better and more-refined tools such as DNA sequencing of pivotal gene regions should clarify the evolutionary ecological patterns that occur in such three-way interactions.

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