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Fungal endophytes which invade insect galls: insect pathogens, benign saprophytes, or fungal inquilines?

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Abstract Fungi are frequently found within insect galls. However, the origin of these fungi, whether they are acting as pathogens, saprophytes invading already dead galls, or fungal inquilines which invade the gall but kill the gall maker by indirect means, is rarely investigated. A pathogenic role for these fungi is usually inferred but never tested. I chose the following leaf-galling-insect/host-plant pairs (1) a cynipid which forms two-chambered galls on the veins of Oregon white oak, (2) a cynipid which forms single-chambered galls on California coast live oak, and (3) an aphid which forms galls on narrowleaf cottonwood leaves. All pairs were reported to have fungi associated with dead insects inside the gall. These fungi were cultured and identified. For the two cynipids, all fungi found inside the galls were also present in the leaves as fungal endophytes. The cottonwood leaves examined did not harbor fungal endophytes. For the cynipid on Oregon white oak, the fungal endophyte grows from the leaf into the gall and infects all gall tissue but does not directly kill the gall maker. The insect dies as a result of the gall tissue dying from fungal infection. Therefore, the fungus acts as an inquiline. Approximately 12.5% of these galls die as a result of invasion by the fungal endophyte.

Key words Fungal endophytes · *Discula quercina* · Gall insects · Parasites · Cynipid wasps

Introduction

The roles of microorganisms are receiving more attention and gaining more credit as agents which mediate the interaction between insects and their host plants (Barbosa et al. 1991; Berenbaum 1988; Letourneau 1988; Wilson 1993). One major group of microorganisms, the fungi, and phytophagous insects show diverse and complex interactions with their host plants. Fungi either help or hinder phytophagous insects. For example, fungi can be insect gut symbionts which help detoxify plant allelochemicals (Dowd 1991; Jones 1984), plant pathogens which turn the plant into a more suitable host for the insect, and insect antagonists which either parasitize the insect or adversely affect its performance or oviposition on the host plant (Barbosa et al. 1991). Fungi which are antagonistic towards insects can be present in the roots as mycorrhizae (Rabin and Pacovsky 1985), on the phylloplane (Ferron 1985), or within healthy leaves and stems as endophytes (Carroll 1988, 1991; Clay 1991a, b; Siegel and Schardl 1991; Siegel et al. 1985; Webber 1981). Since fungal endophytes have been found in almost all plant species where they have been looked for (Petrini 1986), insect herbivores will encounter these microorganisms virtually every time they encounter the host plant. However, endophyte antagonism towards insects has only been demonstrated for the seed-borne endophytes of certain cool season grasses (Clay 1989, 1991a; Funk et al. 1983; Latch et al. 1985), with very few other good examples (Clay et al. 1985; Cubit 1974; Webber 1981). The paucity of reports of antagonism compared with the frequency of insect-endophyte encounters is most likely a reflection of how often fungi are ignored by ecologists and the few investigations which have addressed this question. Similarly, observations of fungi growing on or in close association with insects are often reported but seldom investigated further.

Taper et al. (1986) reported that the major source of mortality of a cynipid gall-forming wasp on California coast live oak was a fungus. Many other workers report the presence of fungi inside both dead insect galls (Carroll 1988; Fernandes and Price 1991, 1992; Lasota et al. 1983; Liu 1991; Weis et al. 1988), and live insect galls (Bissett and Borkent 1988; Weis 1982). The fungi inside live galls are usually mutualists with the insect, either as a food substrate or

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mechanical protection from parasitoid wasps. Fungi associated with dead galls are pathogens, inquilines (inquilines are organisms, including insects and fungi, which may live inside an insect gall but which do not directly parasitize the gall maker, but often feed upon gall tissue), or saprophytes which invade already dead or empty galls. Taper et al. (1986) inferred that the fungus was pathogenic on the larvae, as galls with lower amounts of the fungus often contained live insects. Butin (1992) claimed that the fungi he found inside psyllid, cynipid, and dipteran galls were all pathogens which killed the gall maker. However, the distinction between saprophyte and pathogen, i.e., whether these fungi cause the insect death, has never been experimentally tested. Furthermore, with the exception of Butin (1992), the origin of the fungi is seldom examined.

The fungi found in galls might be leaf endophytes since endophytic fungi are predisposed to grow within the plant tissue. They could enter the gall by growth from the leaf into the gall, direct penetration of the gall from spores on the exterior, or both. Although mode of endophyte entry is probably unimportant in terms of survival of the insect, it could affect oviposition choices made by the female or mechanical properties of the gall. Defence against the endophyte, if present, would differ depending on how the fungus enters the gall. For example, growth from the leaf into the gall might cause the female to oviposite on endophyte-free leaves or parts of leaves, or a mechanical/chemical barrier to the endophyte might be present at the gall-leaf interface.

In this study, I isolated and identified the fungi found inside of the gall on cadavers of three gall-forming insects from well studied systems: (1) *Besbicus mirabilis* Kinsey (Hymenoptera: Cynipidae) on Oregon white oak (*Quercus garryana*) collected in Eugene Oregon (from Evans 1967; Wilson and Carroll 1994); (2) *Dryocosmus dubiosus* Fullaway (Hymenoptera: Cynipidae) on California coast live oak (*Quercus agrifolia*) collected from San Diago California (from Taper et al. 1986); (3) *Pemphigus betae* (Hemiptera: Eriosomatidae) on narrowleaf cottonwood (*Populus angustifolia*) collected from Flagstaff Arizona (from Whitham 1979). I isolated the leaf endophytes from each host plant and compared them with the fungi isolated from galls to determine if the fungi were leaf endophytes. For *B. mirabilis*, I also determined if the dominant endophyte, *Discula quercina* (Westd.) von Arx (Coelomycete), was an agent of mortality or if it was a secondary colonizer of dead galls.

Materials and methods

Isolation of leaf endophytes and gall fungi

Leaf endophytes were isolated by plating healthy, surface-sterilized whole leaves and leaf parts (80 leaves per plant species) on corn meal agar (Difco, Detroit, Michigan, USA) made to half strength. Fungi which grew from the interior of the leaf tissue were transfered onto Potato Dextrose Agar (PDA) (Difco, Detroit, Michigan, USA). Leaves were surface sterilized by immersing in 95% ethanol for 50 sec, 70% ethanol for 1 min, followed by 1.73% sodium hypochlorite solution for 5 min, then rinsed 3 times in sterile distilled water.

The fungus found inside intact *B. mirabilis* galls was identified by breaking open 78 galls then culturing the fungus on PDA. Ninety-three whole intact *Dryocosmus dubiosus* galls were surface sterilized then gently broken open. Using a dissecting microscope, fungal hyphae observed inside the gall, usually on insect cadavers, were transferred to PDA. Fungal hyphae filled the entire *Pemphigus betae* gall cavity. Small amounts of hyphae were transferred to PDA from 26 galls.

All endophytic and gall fungi were grown under the conditions described by Wilson and Carroll (1994).

Fate of *Besbicus mirabilis* galls

Evans (1967) listed sources of mortality for *B. mirabilis*, but did not list fungi as a mortality source. To estimate the relative contribution of different mortality sources of *B. mirabilis*, 1322 galls were collected in October 1990 just before leaf scenescence, and 1065 galls were collected in late summer 1993. Galls were dissected, then placed into four categories as follows:

(1) Mortality caused by an inquiline, *Melissopus latiferreanus* Walsingham (Lepidoptera: Olethreutidae), which enters the gall in late July and feeds on the entire interior of the gall including the inner gall chamber and wasp larva.
(2) Mortality caused by the fungal endophyte. Galls were placed in this category if they contained dead larvae but were fully intact with no breach of the outer gall chamber and were filled with a white or cream-colored fungal mycelium. The exterior color of the gall also turns dark brown when infected.
(3) Healthy. These galls contained live wasp larvae which wriggled if touched. *B. mirabilis* larvae could be distinguished easily from external parasitoids.
(4) Other. This included galls which did not develop and died at a small size, dead galls of unknown cause, as well as those which contained parasitoids.

Causal relationship between the endophyte *Discula quercina*, and *Besbicus mirabilis* mortality

In mid-July 1990, 195 *B. mirabilis* galls from 14 trees (these trees were selected at random from a pool of 65 study trees) were divided into one treatment group and two control groups of 65 galls in each over all trees. As the treatment, 10 µl of a spore suspension (10^6 spores per ml) of the *Discula quercina* endophyte was injected into the outer gall chamber (see "Preparation of Spore Suspension" later). As one control, 10 µl of sterile distilled water was injected into the outer gall chamber. As a second control a hole was poked through the outer gall chamber. To inject the spore suspension and sterile distilled water, a 10 µl Eppendorf pipet with a small hypodermic needle fixed to the tip was used. The needle was flame sterilized in the field before inserting it into each gall to prevent possible transmission of microorganisms from gall to gall, and to prevent contamination of the endophyte spore suspension and sterile distilled water. The fate of each gall was checked visually for signs of browning every 2–3 days until no further change was observed. Previous experience with dissecting many *B. mirabilis* galls shows that browning of the gall exterior is a reliable indicator of *D. quercina* growth inside the gall.

Mode of entry of *Discula quercina* into *Besbicus mirabilis* galls

To examine how the endophyte infects galls, 40 galled but otherwise healthy leaves were removed haphazardly (4 from each of 10 trees selected at random from a pool of 65 study trees) in late July, when no further endophyte infection of leaves occurs (Wilson and Carroll 1994) and galls have attained almost full size, and brought into the laboratory. All galled leaves were surface sterilized as detailed above. Each leaf was placed top side down inside a sterile glass dish lined with moist filter paper to keep humidity high. Of the 40 galled leaves, 20 were randomly selected and each leaf sprayed with 3 ml of a 10^6 spores per ml spore-suspension of *Discula quercina* to determine if gall infection occurs via spores from the exterior of the gall and leaf. The remaining 20 galled leaves were sprayed with sterile distilled water to determine if the endophyte already inside the leaf could grow from the leaf into the gall. All leaves were incubated at room temperature and indirect sunlight for 2 weeks. Galls were then dissected to show where fungal penetration occurred, and to count the number of endophyte-infected galls.

Preparation of spore suspensions

All *Discula quercina* spore suspensions were made as follows. Oak leaves were autoclaved and placed in sterile Petri dishes lined with moist filter paper. Leaves were then inoculated with *D. quercina* and incubated under ambient laboratory conditions. The initial inoculum of *D. quercina* were obtained from surface sterilized leaves which had been left in sterile chambers so the endophyte could fruit on the leaf surface. Conidiomata form and exude spores after 7–10 days on the autoclaved leaves. Using sterile technique the slimy masses of spores can be removed from the conidiomata with a needle and placed into a sterile test tube of distilled water where the slimy masses of spores rapidly disperse into suspension. Spore concentrations were measured with a hemacytometer. Using this method, spore suspensions were free of fungal hyphae and possibly toxic metabolites produced by the fungus growing on the leaves.

Results

The fungi found inside *B. mirabilis* and *Dryocosmus dubiosus* galls were all leaf endophytes (Table 1). However, the fungi isolated from *Pemphigus betae* galls were either insect pathogens or saprophytes. No endophytes were cultured from any of the cottonwood leaves sampled.

The fates of *B. mirabilis* galls were different in the two years sampled (2×4 contingency table analysis, chi-square = 332, $P < 0.0001$). No galls had both *Discula quercina* infections and the lepidopteran inquiline. Many of the apparently healthy galls may have had parasitoid eggs or young parasitoid larvae inside. Therefore, this is an overestimate of the number of healthy galls and an underestimate of parasitized galls. Although a census was not conducted in 1992, observation of the gall population indicated that the incidence of infected galls was much higher than in Table 2 and approached 50%.

Significantly more galls injected with *Discula quercina* spores became infected and died compared to the controls (3×4 contingency table analysis, chi-square = 122, $P < 0.0001$; with the *D. quercina* spore treatment factored out, chi-square = 2.93, $P = 0.23$ for the resulting 2×3 contingency table). Once inside the gall, the injected spores germinate and grow rapidly. The resulting hyphae ramify throughout the gall, eventually leading to the death of the wasp larvae (Fig. 1).

All detached galled leaves ($n = 20$) in the treatment sprayed with *D. quercina* spores and control detached galled leaves ($n = 20$) sprayed with sterile distilled water, had prolific *D. quercina* growth both inside galls and on the leaf veins and lamina. Since the growth of *D. quercina* inside *B. mirabilis* galls is very characteristic, subculturing the fungus inside the galls to confirm its identity was not necessary. Treatment and control galls became infected and turned dark brown after 8–12 days following spraying. Dissection of the galls revealed:

(1) Fungal hyphae inside the central gall chamber with dead larvae. Some larvae were still alive but appeared flaccid and showed little response to touch compared to healthy looking larvae.

Table 1 Fungi isolated from leaf tissue and insect galls for each host plant/insect pair (+ present, – not isolated)

Host tree/galling insect pair	Fungus	Leaf tissue	Insect gall
Quercus garryana/ *Besbicus mirabilis*	[a]*Discula quercina* (West.) von Arx	+	+
	[c]*Apiognomonia* sp.	+	–
	[b]*Fusarium* sp.	+	–
	Sterile mycelia 1	+	–
	Sterile mycelia 2	+	–
Quercus agrifolia/ *Dryocosmus dubiosus*	[a]*Discula quercina*(West.) von Arx	+	+
	[a]*Cryptosporiopsis quercina*	+	+
	[b]*Aureobasidium* sp.	+	+
	[a]*Phomopsis* sp.	+	+
	Sterile mycelia 3	+	+
Populus angustifolia/ *Pemphigus betae*	[b]*Verticillium lecanii* (A. Zimmerm.) Viégas	–	+
	[b]*Cladosporium cladosporioides* (Fres.) de Vries	–	+
	[b]*Penicillium* sp.	–	+

[a] Coelomycetes (see Sutton 1980)
[b] Hyphomycetes (see Ellis 1971)
[c] Ascomycete: Diaporthales (see Barr 1978)

Table 2 Fate of *B. mirabilis* galls

Fate of gall	Number of galls [a]1990	[b]1993	Percentage of galls 1990	1993
Mortality caused by a lepidopteran inquiline	846	316	64%	30%
Mortality caused by the *Discula quercina*	146	154	11%	15%
Healthy galls	263	557	20%	52%
Other	67	37	5%	3%

[a] $n = 1327$
[b] $n = 1065$

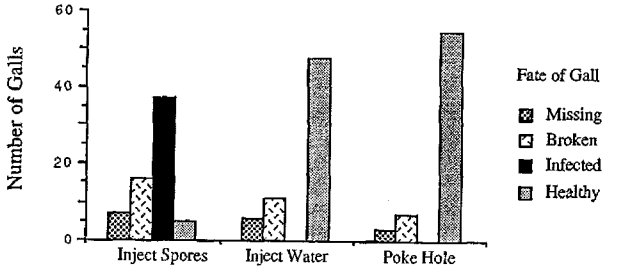

Fig. 1 Fates of *Besbicus mirabilis* galls in each of three treatments. Broken and missing galls were caused by humans and possibly birds as the galls were conspicuously labeled

(2) Galls at an earlier stage of infection had hyphae concentrated mostly along the dense aggregation of threads which directly connects the leaf vascular system with the central gall chamber.

Discussion

Occurrence of fungi inside insect galls: agents of mortality or saprophytes?

Discula quercina is the dominant leaf endophyte of both *Quercus garryana* and *Q. agrifolia*, and is also a fungal inhabitant of their respective cynipid galls. The results of the injection and spraying experiments with *Q. garryana*, suggests that under certain conditions the endophyte readily grows from the leaf into the live galls. Furthermore, fungal spores on the surface of the plant tissues do not increase mortality or the speed of infection.

The frequency of saprophytic infections of *D. quercina* in *B. mirabilis* might be very low as galls killed by the activities of a lepidopteran inquiline (Table 1) were never infected with *D. quercina*. In addition, galls at a very early stage of fungal penetration frequently contain live insect larvae. Thus, *D. quercina* which infects *B. mirabilis* is acting as a parasite, invading insect galls, thereby causing gall mortality. The mutual exclusion of the lepidopteran inquiline and fungal endophyte from galls can be explained by a lottery model (Chesson 1991). The lepidopteran would not invade galls already infected with *D. quercina* since the gall tissue has become spoiled. Similarly, the endophyte would not invade an already dead, and usually dried or completely emptied gall, which had been fed upon by the lepidopteran inquiline.

The nature of the interaction (pathogenic or saprophytic) between *Discula quercina* cultured from the *Dryocosmus dubiosus* galls (Table 1) is unresolved. Similarly, whether *Discula quercina* [reported as *Gloeosporium quercinum,* in Butin (1992)] found inside the cynipid gall wasp *Neuroterus numismalis* Oliv. on *Quercus robur* in Germany and Austria (from Butin 1992) is a pathogen or saprophyte is unknown, although it would be reasonable to propose a parasitic relationship for *Discula quercina* in both instances. Whether the other endophytes cultured from *Dryocosmus dubiosus* galls act in the same manner is unknown; they might be secondary invaders of galls killed by *Discula quercina*. *Aureobasidium* sp. and *Phomopsis* sp. are both common, widespread occupants of plant surfaces: however, the former has been found inside psyllid galls on *Q. robur* (Butin 1992).

The fungi found inside of *Pemphigus* galls, however, were not leaf endophytes. The origin of these fungi is most likely from air-borne spores outside of the galls. *Penicillium* sp. is a very common, cosmopolitan genus of fungus present in almost every environment and is probably a secondary invader of the gall, perhaps growing on aphid sap or insect cadavers not expelled from the gall. *Cladosporium cladosporioides* is a common species of mild plant pathogen and is commonly found on aphid cadavers (see catalogue of fungi in the USDA-ARS culture collection Boyce Thompson Institute at Cornell University, New York). *Verticillium lecanii* is a known insect pathogen of several different species of insect. However, in this case *V. lecanii* may have been a mycoparasite on *C. cladosporioides* (R Humber, personal communication), but whether it infected the galls and killed the aphids and then turned mycoparasitic on *C. cladosporioides* is unknown. All of these fungi could have entered the gall easily via the opening to the outside following gall dehiscence.

Entry of *Discula quercina* into the gall

Two lines of evidence suggest that the mode of endophyte entry is by growth from the leaf into the gall rather than penetration of the outer gall chamber. First, spraying the detached galled leaves with endophyte spores did not decrease the time nor increase efficacy with which the endophyte entered live galls. Dissection of these galls early in the stages of fungal penetration revealed that fungal hyphae were only present in the dense aggregation of threads which connect the central chamber with the leaf veins. Second, the spores of the endophyte are rain dispersed (Wilson and Carroll 1994). Since galls still become infected after the period of heavy rainfall when the summer drought begins, both fungal activity and an inoculum source of the endo-

phyte is low to nonexistent at this time, although penetration of the gall by spores on the gall surface might take several weeks.

It is perhaps somewhat perplexing that although all galls on detached leaves in the moist chamber spraying experiment became infected, only an average of 12.5% of galls became infected out in the field. Wilson and Carroll (1994) showed that *Discula quercina* has very little growth activity once it has infected the leaf. Spores germinate, then penetrate the leaf but do not grow away from that site of infection. Thus, out in the field, leaves with galls may become endophyte infected but because the endophyte has only very limited growth activity inside the leaves, very few galls become colonized. However, when leaves are detached, endophyte growth within the leaf is initiated leading to systemic colonization of leaf and gall tissue. Wilson and Carroll (1994) also reported that trees which are severely light stressed showed activation of *D. quercina* growth within the leaf. Other stress factors might have similar effects so could lead to gall colonization.

The difference in galls fates between 1990 and 1993 (Table 2) is probably caused by the difference in time of year galls were sampled. In contrast to 1990, galls in 1993 were sampled before the activities of the lepidopteran inquiline had completely stopped. Accordingly, lepidopteran inquiline-caused mortality was lower and the number of healthy galls greater than in 1990. Interestingly, endophyte-caused mortality was higher in 1993 than in 1990 (chi-square = 6.44, $P < 0.05$) and could have been higher at the end of the season. Coincidentally, this increased endophyte-caused mortality occurred in a year with heavier than usual rainfall which would have favored endophyte infection (Wilson and Carroll 1994).

Mode of endophyte-caused mortality

Toxins produced by antagonistic endophytes are usually identified as the causative agent of endophyte-mediated antagonism towards insects (Carroll 1991; Dahlman et al. 1991; Johnson et al. 1985; Prestidge and Gallagher 1988; Rowan and Gaynor 1986; Siegel et al. 1987). Although toxin production by endophytes is responsible for the antiherbivore properties of endophyte-infected grasses, fungal produced toxins might not be the causative agent of insect death here. Instead, mortality is probably caused by insect starvation and the invading endophyte is acting like a fungal inquiline. When the fungus invades galls containing larvae which are still feeding, that is, before the gall begins to dry out, the insect always perishes. However, late in the season galls are occasionally found which contain prolific fungal growth inside both the outer and inner gall chamber but which also contain a healthy late instar larva. These galls, and similar galls found beneath trees in mid-winter, usually produce a healthy adult wasp when brought into the laboratory. If toxins were important, one would expect all larvae which were encased in a gall lined with fungal hyphae to perish, especially if the insect-endophyte contact is over a long period of time as is often the case when galls are invaded in August but wasp emergence is in January. Alternatively, however, later instars could be more resistant to toxins as suggested by Chew (1980) and Courtney (1981).

The endophyte probably does not directly invade the insect larvae as many entomopathogens do (Ferron 1985), since microscopic examination of recently dead larvae showed that cadavers are not impregnated with fungal mycelium. When the endophyte invades the gall, the first gall structures infected are the threads which supply the nutritive cells lining the inner gall chamber. As a result of cutting off the nutrient supply from the leaf to the gall and infecting all the nutritive tissue, the feeding larvae will starve to death but post-feeding instars will survive.

Discula quercina occupies a large geographical area, from Europe to N. America, has a broad host range (Toti et al. 1992), and is present inside cynipid galls over its range of different habitats. Many different gall insects utilize the same hosts as fungal endophytes but their effects on the insects is largely unknown. *Discula quercina*- caused mortality is the second highest source of mortality for *B. mirabilis* and the highest for *Dryocosmus dubiosus* (Taper et al. 1986). How will this affect the distribution and abundance of the affected insects? Taper et al. (1986) suggested that ovipositing females should chose high tannin leaves as fungal growth is inhibited by tannins; indeed, fungal-caused mortality was lower on high tannin leaves. Thus, gall insects could avoid endophyte, caused mortality by avoiding high "endophyte space". Chemical properties of the gall might further lessen fungal-caused mortality as insect galls can be up to 60% tannins (Russo 1983). In addition, morphological adaptations of the gall might be to defend against endophyte attack. For example, many insect galls are spatially distinct from the infected leaf tissue and connected only at a small junction thereby spatially separating "insect space" from "endophyte space". The endophyte would then have to grow throughout the plant tissue into gall tissue to affect the insect.

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