FUNGAL ENDOPHYTES IN STEMS AND LEAVES:
FROM LATENT PATHOGEN TO MUTUALISTIC SYMBIONT

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ABSTRACT

Endophytes are fungi that form inapparent infections within leaves and stems of healthy plants. Closely related to virulent pathogens but with limited, if any, pathogenic effects themselves, many endophytes protect host plants from natural enemies. Animal herbivores and, in some cases, pathogenic microbes are poisoned by the mycotoxins produced by endophytes. "Constitutive mutualism" is the relatively faithful association, usually with grasses, of endophytes that infect host ovules and are propagated in host seed; substantial fungal biomass with probable high metabolic cost develops throughout the aerial parts of the host plant. "Inducible mutualist" endophytes are not involved with host seed and disseminate independently through air or in water. Infecting only vegetative parts of the host and remaining metabolically inactive for long periods with relatively little fungal biomass, inducible mutualists grow rapidly and produce toxins against herbivores when damaged host tissues provide new sites for infection. I surmise that endophytes may be as common among plants as are mycorrhyzae.

Key words: fungal endophytes; latent infection; mutualism; pathogen; symbiosis.

INTRODUCTION

A bounteous and succulent harvest of fruit is expertly picked, carefully packed, and shipped to a distant market; on arrival the fruit are found to be blotched, pitted, softened, or rotted. In countries without advanced agricultural technologies, postharvest losses of perishable crops have been estimated at levels as high as 50% (Eckert and Ogawa 1985). Fungi that form latent infections in unripe fruit predominate as a cause of postharvest fruit rots. Fungal infections with long latent phases are not, however, restricted to fruit. Many leaf pathogens that infect the host just as the young leaves emerge from the bud do not form lesions until months later. For example, in one species of *Rhabdocline* on Douglas-fir, 2 yr may elapse between infection and development of a fruiting body on the infected needle (Parker and Reid 1969, Funk 1985). Recent reports of long latency periods in diseases of cranberry (Weide-

mann and Boone 1984), soybeans (Kulik 1984), and oilseed rape (Nathaniels and Taylor 1983) suggest that the phenomenon may not be uncommon among leaf and stem pathogens.

ENDOPHYTE TAXONOMY AND DISTRIBUTION

Completely asymptomatic fungal infections also exist. Fungal hyphae occur within healthy tissues among plants as diverse as *Casuarina* (Bose 1947), *Helianthemum* (Boursnell 1950), and *Lolium* (see Clay 1986 and 1988). More recent studies based largely on pure culture of surface-sterilized stems and leaves have revealed an astounding diversity of fungal species existing subcuticularly or within the tissues of many kinds of healthy plants. (Carroll and Carroll 1978, Luginbühl and Müller 1980, Petrini and Dreyfuss 1981, Petrini 1984, Clay 1986, Fisher et al. 1986, Petrini and Fisher 1986). Such fungi have been called endophytes, a term long used to indicate fungal residence within plant tissues, rather than on plant surfaces.

Taxonomically, endophytes are with few exceptions Ascomycetes, but within the Ascomycetes they are very diverse, including Loculoascomycetes, Discomycetes, and Pyrenomycetes (Petrini 1986). Certain genera of fungi always appear in endophyte censuses regardless of the host plant sampled. Chief among these are *Cryptocline, Cryptosporiopsis, Leptostroma, Phomopsis,* and *Phyllosticta.*

Endophytes can infect virtually 100% of a host population, but many infect a far smaller fraction; some are rare (Carroll and Carroll 1978, Petrini 1986). Endophytes can be transmitted from one generation to the next through the tissue of host seed or vegetative propagules. Except in the grasses, however, most endophytes appear to be transmitted horizontally, external to host tissues, by spores; climate can greatly influence spore germination and resultant infection frequency of host plants. Carroll and Carroll (1978) showed the infection frequencies of endophytes in Douglas-fir collected over a wide geographical range to be positively correlated with annual precipitation (rain, mist, fog drip) and negatively correlated with elevation.

Many endophytes produce masses of slimy conidia, a characteristic often associated with rain dispersal.

A few cases of strict host specificity for endophytes are known. For example, *Rhabdocline parkeri* occurs only on Douglas-fir and not on any other sympatric conifer in the Pacific Northwest (Carroll and Carroll 1978, Sherwood-Pike et al. 1986), but such specificity is the exception; broader host ranges are more commonly observed. For example *Phyllosticta* sp. 1 occurs frequently on Douglas-fir and on all species of true fir examined throughout North America. Although host-specificity among races of this fungus cannot be ruled out, all isolates appear morphologically identical. In another example, for ericaceous plants in the Swiss Alps, host specificity of endophytes is evident only at the family level (Petrini 1985). Certain endophytes appear to be host-neutral! Thus the *Geniculosporium* state of *Hypoxylon serpens* has turned up as a minor component of the endophyte flora in almost every host species sampled in depth from a number of sites.

ENDOPHYTES AS MUTUALISTIC SYMBIONTS

In view of the commonness of fungi without overt pathogenicity, a mutualistic modus vivendi between fungus and host plant might well be surmised. Carroll and Carroll (1978) proposed that coniferous needle endophytes could serve to decrease leaf palatability for grazing insects and to antagonize leaf pathogens. Since then considerable evidence has accrued in favor of these hypotheses.

Herbivore resistance

At least one casual observation as well as several careful studies have now shown that leaf and stem endophytes may militate against herbivores. Diamandis (1981) reported that *Pinus brutia,* when planted outside its normal range in Greece, was attacked by both the pine processionary caterpillar and the needle blight *Elytdroderma torres-juanii.* However, caterpillars avoided needles previously infected by the fungus, a conspicuous example of interference between a latent pathogen (and probable endophyte in a more favorable climate) and a grazer.

Another example, limned in more detail, has been provided by Cubit (1974). The marine green alga *Enteromorpha vexata,* found along the coast of southern Oregon, was heavily grazed by marine mollusks unless infected by an endophytic ascomycete. Only 0–20% of the algal thalli with the fungus were grazed, whereas 100% of the uninfected thalli were eaten. Indeed, only the infected thalli survived the summer months, when grazing pressure was heaviest.

In three systems the host-endophyte-grazer relationship has been studied intensively. In all three, the life cycles of the grazers and infection cycles of the endo-
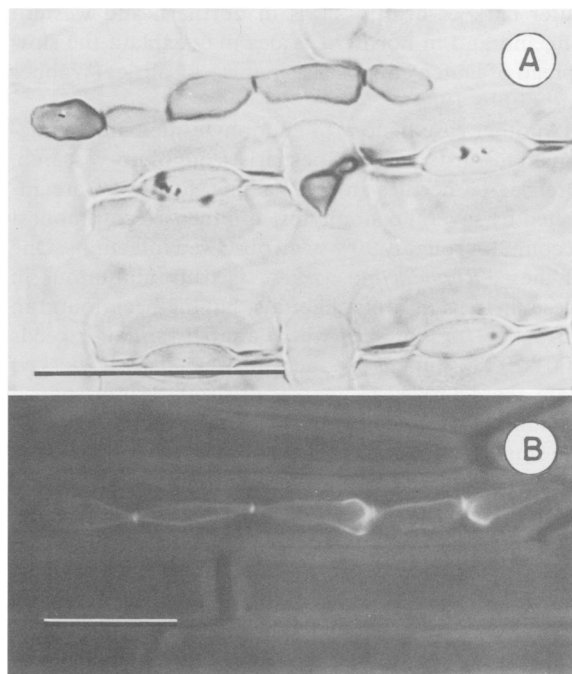

FIG. 1. Intracellular infections of *Rhabdocline parkeri* in cleared Douglas-fir needles. Each bar = 25 μm. (A) Light micrograph of trypan blue–stained hypha in epidermal cell on abaxial surface. (B) Epiflourescence micrograph of calcofluor-stained hypha in epidermal cell on adaxial surface. Photographs provided courtesy of Jeffrey Stone.

phytes are well understood. The locations of the fungi within host tissues are known, something is known of the endophyte infection frequencies in natural stands of the host plants, and a chemical basis for herbivore deterrence is known or is currently under investigation. Endophytes of grasses, reviewed at length by Clay (1988), constitute the longest recognized and best documented case histories. The fungi are all allied to the Clavicipitaceae; many form systemic infections that are transmitted vertically through the host seed.

Elm bark beetles interact with the endophyte *Phomopsis oblonga.* In elm trees attacked by the beetle, the inner bark may be invaded by *P. oblonga;* colonization by the fungus clearly disrupts beetle breeding and leads to a decline in beetle populations (Webber 1981). Under laboratory conditions beetles clearly preferred control logs over those infected by *P. oblonga,* and forced breeding in the infected logs resulted in a drastic curtailment of emergent progeny. Several chemical compounds that hinder beetle performance are produced by the fungus alone (Claydon et al. 1985). *Ceratocystis ulmi,* causative agent of the Dutch elm disease, is vectored by bark beetles. The widespread occurrence of *P. oblonga* as a natural inhabitant in the

outer bark of healthy elms in northern and western England and in northern Wales may explain the slow spread of Dutch elm disease in these localities (Webber and Gibbs 1984).

Another case history of endophyte-mediated antagonism towards an insect pest arises out of my research. Douglas-fir needles in the Pacific Northwest are infected by several endophytes, and the two commonest account for roughly 90% of all observed infections. One of these, *Rhabdocline parkeri*, is truly ubiquitous in these fir trees in moist habitats, having been found in virtually 100% of sites where annual rainfall exceeds 100 cm. This fungus produces an asexual *Meria parkeri* state characterized by masses of slimy peanut-shaped conidia produced on conidiophores growing through the stomata of senescent needles (Sherwood-Pike et al. 1986). In the Pacific Northwest the *Meria* conidial state first appears on freshly fallen needles from mid-October through November. The slimy conidia are dispersed by rain drops from needles lodged in the canopy; during this period the conidia initiate new endophytic infections, each conidium penetrating a single epidermal cell on a healthy needle and forming a single infection hypha limited to that epidermal cell (Fig. 1A and B; see also Sherwood-Pike et al. 1986, Stone 1988, Stone and Carroll 1988). The hypha grows further only as the needle senesces. Because needles infected in their 1st yr can live as long as 9 yr, the fungus has an extraordinary latent period of up to 8 yr. Early in December *R. parkeri* may produce minute sparse ascocarps on recently fallen needles beneath infected trees. Germination of ascospores has not been observed, and their role in the infection cycle is still unknown.

Douglas-fir needles may be attacked by any of three species of gall midges in the genus *Contarinia* (Condrashoff 1962). The adult flies emerge at bud burst in late spring. After mating, female flies lay clusters of minute red eggs among needles emerging from the buds. Each larva chews a hole in a young needle and ensconces itself within the needle tissue. Survivors feed throughout the summer; by September a substantial gall has formed around each surviving larva. Late in the autumn, the third instar larvae emerge from the galls and fall to the ground, where they overwinter. Pupation occurs in the ground during April.

Conidia from the *Meria* state of *R. parkeri* infect *Contarinia* galls in October. On infected galls the fungus quickly sporulates prolifically. Indeed, in *Contarinia*-infested stands, infected galls probably represent the major source of inoculum for new needle infections. Studies in the fall of 1983, 1984, and 1986 provided consistent evidence for antagonism between the fungus and the insect. The initial 1983 study paired infected with uninfected samples of ≈50 galls from each of eight trees at a single site, and mortalities of parasitoid-free

larvae were compared. The results showed that mortality was clearly higher in the infected sample (Carroll 1986). Because the fungus does not invade the bodies of the living larvae, fungal toxins are suspected to be responsible for larval death. Miller (1986) has reported that at least one clone of *R. parkeri* produced compounds that caused significant growth reduction and mortality in spruce budworm grown in the laboratory.

Other correlations between fungal infection and insect mortality within galls are known for *Adelges abietis* on white spruce, with galls infected by *Cladosporium sphaerospermum* (Lasota et al. 1983). The cynipid gall wasp *Dryocosmus dubiosus* on California live oak is involved with a surprising positive correlation between leaf tannin content and insect survival (Taper et al. 1986, Taper and Case 1987). Fungi are the major cause of mortality for this gall-making wasp. Fungal growth on the galls is negatively correlated with high leaf tannin content. Unfortunately in neither of the above cases is the mycology well understood. The mode of fungal persistence on the plant when galls are absent is unknown, and the source of fungal inoculum and the fungal infection cycle need to be elucidated. In the case of the live oak the fungus remains unidentified. Is there a reservoir of fungal biomass within tissues of the host plants themselves?

Antagonism towards microbial pathogens

Microbial infection of uncongenial hosts can protect against at least some virulent pathogens (Matta 1971). Asymptomatic *Fusarium* infections described by Matta certainly qualify as endophytic and can "immunize" host plants against fungal pathogens. Unequivocal examples of endophyte-microbe antagonisms are few. One such example is for species of *Lophodermium* in Scots pine needles (Minter 1981). One of these fungal congeners, *L. seditiosum*, is a pathogen on young trees, causing serious premature needle loss. Another species, *L. conigenum*, fruits only after needles have died from old age or another cause and hence behaves as an endophyte. The pathogen colonizes and fruits on needles attached to fallen branches only when *L. conigenum* is absent from the forest; when *L. conigenum* is present, the pathogen is excluded from this microhabitat. In populations of Scots pine of mixed age, then, we might expect the presence of *L. conigenum* in needles of older trees to reduce the inoculum of *L. seditiosum* in the stand and thus reduce infection of young trees by the pathogen.

Possible antagonism by the grass endophyte *Acremonium coenophialum* towards several grass pathogens has been recently reported (White and Cole 1985). Culture filtrates of *A. coenophialum* inhibited in vitro growth of the recognized grass pathogens *Nigrospora*

sphaerica, Periconia sorghina, and *Rhizoctonia cerealis.*

Strategies of endophytic mutualism

Two patterns emerge. The first, constitutive mutualism, is typified by the grasses and their endophytes. Here, the endophyte is carried through the seed, develops a systemic infection throughout the aerial parts of the plant involving a substantial fungal biomass, and is always present in the lines that carry it. Potent fungal toxins may deter herbivores, which show a preference for uninfected plants, giving immediate and direct benefits to the endophyte's host. The costs to the plant may be high, involving energy for fungal metabolism and, sometimes, loss of reproductive function (Clay 1988). The alga–ascomycete association described by Cubit (1974) conforms to this pattern; other seed-borne endophytes such as that in *Casuarina* (Bose 1947) should also behave in this fashion.

Inducible mutualism involves a much looser association between endophyte and host, as with *Rhabdocline parkeri* in Douglas-fir and *Phomopsis oblonga* in elm. Abundance of the endophyte may vary greatly with the geographical distribution and age of the host (Carroll and Carroll 1978, Webber and Gibbs 1984). The fungi normally live in senescent or metabolically inactive tissues such as bark or epidermis, and colonize vital tissues only when the host is wounded or stressed by insect or pathogen attack. The endophyte serves not as a direct deterrent to herbivores, but rather as an inoculum source. Infection of injured tissue results in death or decreased fitness of the herbivore and a general decrease in levels of herbivory among populations of the host plant. Sources of inoculum are probably so scattered and inapparent as to be beyond detection by an insect and therefore not a factor in herbivore host selection. In such situations benefits to an individual host are diffuse and the metabolic costs probably small. Benefits to a host population, however, may be high.

Generality of endophytic mutualism

Endophytic mutualism may prove to be as prevalent as mycorrhizal mutualism. What characteristics might flag the presence of mutualism among endophytes? I suggest the following.

1) The endophyte is ubiquitous in a given host over a wide geographic range and causes minimal symptoms of disease in the host plant.
2) Vertical transmission of the fungus occurs through the host seed or vegetative propagules. If seed transmission does not occur, horizontal transmission must be efficient.
3) The fungus grows throughout host tissues. If infection units are dispersed, they should be numerous; if confined to a particular organ, a high proportion of the organs should be infected.
4) The fungus produces secondary metabolites likely to be of antibiotic or toxic nature.
5) The endophyte is taxonomically related to known herbivore or pathogen antagonists (e.g., *Acremonium, Phomopsis, Lophodermium*).

Given these criteria, some of the published host–endophyte records might repay further investigation. Endophytes of *Casuarina equisetifolia* (Bose 1947) and *Helianthemum chamaecistus* (Boursnell 1950) are vertically transmitted through the seed and are otherwise inapparent in the plant. *Acremonium curvulum* in *Myriophyllum* (Andrews et al. 1985) is ubiquitous and inapparent until host senescence and belongs to a genus of known endophytic mutualists in grasses. *Ascocoryne sarcoides* from healthy stems of *Picea abies* (Roll-Hansen and Roll-Hansen 1979) produces a novel terphenylquinone of possible antibiotic activity (Quack et al. 1982). *Cryptosporiopsis* sp. endophytic in *Vaccinium myrtillus* (Fisher et al. 1984) produces an antibiotic. All of the numerous endophytic members of the Hypodermataceae and Hemiphacidiaceae as well as species of *Phomopsis* and *Acremonium* beg for further investigation by virtue of taxonomic affinity with known mutualists.

ALTERNATE SCHEMES OF ENDOPHYTISM

Not all reported endophytes are known to deter pests. However, more subtle relationships than outright biochemical synergy may pertain among symbionts. For example, a high proportion of the endophytes isolated from *Ulex* spp. (gorse) in Great Britain fruit on dead gorse spines. Fisher et al. (1986) suggest that endophytes may hasten senescence and death of older photosynthetic organs. *Ulex* species are adapted to periodic fires, usually resprouting rapidly from the base (Tansley 1939). Endophyte-hastened senescence might enhance the buildup of dead wood and increase the likelihood of a burn. Again for *Ulex* species, a further 20% of the fungal isolates reported by Fisher et al. (1986) belong to the Ascomycete genus *Sporormiella,* normally found on dung. Wicklow (1975) has demonstrated that a group of coprophilous Ascomycetes, including *Sporormiella,* become active in postfire prairie soils; apparently such organisms can exploit this alternative habitat when ascospore germination is stimulated by heat. I suggest that the normally coprophilous endophytes in *Ulex* may have adopted a similar strategy. Rapid growth of fire-adapted microorganisms after a burn and concomitant immobilization of dissolved nutrients might prove useful for surviving plants as a means for reducing postfire nutrient leaching.

EVOLUTION OF ENDOPHYTES

Why endophytes?

Acquired chemical defense appears to be a common basis for endophytic associations between plants and fungi, but many higher plants themselves produce potent and multifarious chemical defenses (Bell 1981, Bailey and Mansfield 1982, Kuć and Rush 1985, Harborne 1986). Why should some plants form mutualistic associations to accomplish the same end?

One explanation emerges from a comparison of the generation times of endophyte host plants with those of insect and pathogen pests. The importance of chemical heterogeneity among plant populations as a defense against herbivorous insects has been repeatedly stressed in the recent literature (Berenbaum 1981, Denno and McClure 1983, Strong et al. 1984, Berenbaum et al. 1986). Such heterogeneity seems to be highly heritable (Berenbaum et al. 1986) and consequently must arise through the processes of meiosis and somatic mutation. Trees such as Douglas-fir may live 1000 yr in tracts with favorable soil that escape fires; even shorter-lived trees may easily live 100 yr. During a tree's lifespan its genotype is fixed, with little variation possible in its particular mix of allelochemicals and other defenses. Conversely, univoltine insects go through a single generation each year, and many insects and pathogens achieve multiple generations annually. In such situations one might expect an insect or pathogen to specialize in overcoming the defenses of a single host individual or clone. Edmunds and Alstad (1978) have demonstrated such specialization for a scale insect on pine. Indeed, the pressures for specialization in this case were thought to be so great that extinction was predicted for the insect deme when its host tree died.

Somatic mutation within long-lived trees is a possible cause of within-crown variation, which could deter hyperspecialized herbivores and pathogens (Price 1980, Whitham and Slobodchikoff 1981, Whitham 1983). Gall-forming aphids on poplar behave as if such mutation had occurred (Whitham 1983). Schultz (1983) has reviewed the evidence for crown heterogeneity within single trees and concludes that, although such variation exists and is significant, it may arise by means other than somatic mutation. Hall and Langenheim (1986) have examined within-tree spatial variation in monoterpenes for one of the longest-lived of trees, *Sequoia sempervirens,* and find no evidence for somatic mutation. Karban (1987) has considered the same problem and suggests that a pest attack early in the life of a tree could variably and permanently alter the defensive chemistry of an individual such that subsequent pest outbreaks would be forestalled.

I propose that a short-cycle endophyte is another likely cause of heterogeneity within long-lived plants to the challenge presented by short-cycle insects. Inducible mutualism may be particularly appropriate to such challenges, as endophyte strains may produce different repertoires of mycotoxins. Hosts might accommodate different endophyte species in response to challenges from different herbivorous insects.

The path to endophytism

All available evidence suggests that endophytes have evolved directly from plant pathogenic fungi. Apparently innocuous endophytes may cause pathogenic symptoms when the host is stressed (Millar 1980, Andrews et al. 1985), and many endophytes on coniferous hosts show the limited substrate use of parasitic fungi (Carroll and Petrini 1983, Stone 1986). In agricultural situations the distinction between latent pathogen and endophyte becomes fuzzy (Nathaniels and Taylor 1983, Kulik 1984). Pathogens of crops may exist endophytically in weeds growing in the same fields (Hepperly et al. 1985). If the transition from pathogen to endophyte is easy, modern agricultural practices should encourage pathogenic facets of latent fungal infection. Where pests are controlled chemically, endophyte-tolerant hosts would derive no benefit from the association, and the accommodation between fungus and plant would be disrupted as natural selection favored endophyte-intolerant hosts.

Taxonomic evidence further supports a close relationship between endophyte and pathogen. Frequently endophytes are sister species to virulent pathogens on the same or closely related hosts. Thus, *Acremonium coenophialum,* an important grass endophyte, is very closely related to *Epichloë typhina,* a pathogen (Clay 1988). In Douglas-fir the endophyte *Rhabdocline parkeri* bears close morphological similarity to two virulent needle pathogens, *R. wierii* and *R. pseudotsugae* (Funk 1985, Sherwood-Pike et al. 1986). The needle pathogen *Lophodermium seditiosum* was once lumped with the two endophytic species *L. conigenum* and *L. pinastri* in a single taxon (Minter et al. 1978, Minter and Millar 1980).

Fungi preadapted for mutualism would include pathogens with latency in their hosts and mycotoxin production. Many fungi on grains and other seeds produce potent mycotoxins active against both vertebrates and insects (Ciegler et al. 1971, 1972, Wyllie and Morehouse 1977); these have been interpreted as a form of fungal interference competition for a valuable resource (Janzen 1977). Possible intermediates in this evolutionary process include the inapparent *Fusarium* species (Matta 1971). The pathogens that decrease conversion efficiencies by herbivores or lessen herbivory are also candidates for proto-endophytism (Kingsley et al. 1983, Karban et al. 1987). Further, the well-known reciprocal biochemical warfare between fungal pathogens (Bell

1981, Durbin 1981, Bailey and Mansfield 1982, Daly and Knoche 1982) and their hosts might deter herbivory and set the stage for the evolution of endophytic mutualism.

For constitutive endophytes the above scenario involves straightforward natural selection operating on individuals, symbiosis with mutual benefit. In inducible endophytic mutualisms, however, the benefits are more diffuse and delayed. Thus, in the elm–*P. oblonga* example lineages but not individual trees are protected from beetle attack by the endophyte. By the time *P. oblonga* is active, the tree is likely to be infected with *Ceratocystis ulmi* and moribund. The benefits accrue to neighboring trees and descendents from decreased beetle populations. In Douglas-fir, *Contarinia* sp. flies are a negligible problem for old-growth trees, although they may cause significant damage in stands of seedlings or young trees. Nevertheless, needles of old trees are heavily infected with the endophyte, and such infections presumably serve as an inoculum source for adjacent stands of young trees in recently burned areas or clearcuts. Again, the benefit is spread among individuals and generations. Diffuse mutualism is also well exemplified by the *Lophodermium* spp. endophytes on Scots pine discussed above. Although the pathogen causes no damage to older trees, those trees harbor another endophyte that excludes the pathogen and indirectly controls the disease on adjacent seedlings.

Kin selection, a form of genic selection whereby organisms sharing a high proportion of the same genes show altruistic behavior (Wilson 1983), is a likely mechanism for the evolution of the diffuse mutualistic effects of inducible endophytes. Wind dispersal often carries tree seed relatively short distances (Spurr and Barnes 1980), and adjacent individuals may show a high degree of genetic similarity, allowing mutualisms dependent on kin selection to evolve and to work effectively. Other explanations are possible. For example, demes of flies could be adapted to individual trees, causing selection to operate at the level of individual trees. The Cecidomyiid *Thecodiplosis japonensis* does cluster infestations around individual trees (Sone and Furano 1982).

ENDOPHYTE RESEARCH: AN OPPORTUNITY FOR OPPORTUNISTS

The widespread occurrence of endophytes in a variety of higher plants has gained recognition only rather recently. With this recognition will surely come explanations of previously mysterious or unappreciated phenomena in the realm of plant–insect interactions. The following are offered merely as samples.

1) Endophytes may prove a common cause of gall-insect mortality. Where life tables of gall insects have

been constructed and a large component of mortality remains unexplained, fungal parasitism of the galls by endophytes should be suspected. For example, fungal endophytes in *Baccharis* leaves may cause a significant fraction of the unexplained mortality of *Rhopalomyia californica* larvae reported by Ehler (1982).

2) Endophytes may be involved with the cyclical fluctuations in populations of herbivorous insects. Miller (1986) reports that both endophytes and epiphytes of balsam fir colonize and proliferate in wounded tissues of needles. Toxins in needles could have built up to the point where the foliage became toxic to insects and outbreaks were terminated. A subsequent decrease in endophyte inoculum and the natural attrition of infected needles would leave the forest vulnerable to insect outbreaks again after a lapse of a few years.

3) Spatially patchy insect outbreaks in certain parts of a host's range and not in other areas remains to be satisfactorily explained (Strong et al. 1984).

Beyond specific problems, plant–endophyte associations may prove excellent model systems for the study of the evolution of microbial symbioses. If endophytes have evolved from pathogens, the toxins active against animals are likely to have evolved from toxins against plants. A detailed examination of the secondary products in related plant pathogens and endophytes (e.g., *Rhabdocline* spp.) would provide a fascinating history of biochemical evolution at work as the targets of toxins changed from plants to animals. Whatever discoveries lie in the future, the truly elegant investigations will result from collaborative efforts of people who can bring the knowledge and skills of the botanist, entomologist, mycologist, and secondary-products chemist to bear on a single model system. To succeed in the endophyte research, ecologists, like the endophytes themselves, will have to operate in a mutualistic mode.

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