Proc. Natl. Acad. Sci. USA
Vol. 77, No. 4, pp. 2113–2118, April 1980
Ecology

Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants (A Review)

(coevolution/tropical ecology/fungi/legumes/soil nutrients)

D. W. MALLOCH*, K. A. PIROZYNSKI†, AND P. H. RAVEN‡

*Department of Botany, University of Toronto, Toronto, Ontario M5S 1A1 Canada; †Paleobiology Division, National Museums of Canada, Ottawa, Ontario K1A 0M8 Canada; and ‡Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166

Contributed by Peter H. Raven, October 8, 1979

ABSTRACT Mycorrhizae, the symbioses between fungi and plant roots, are nearly universal in terrestrial plants and can be classified into two major types: endomycorrhizae and ectomycorrhizae. About four-fifths of all land plants form endomycorrhizae, whereas several groups of trees and shrubs, notably Pinaceae, some Cupressaceae, Fagaceae, Betulaceae, Salicaceae, Dipterocarpaceae, and most Myrtaceae form ectomycorrhizae. Among legumes, Papilionoideae and Mimosoideae have endomycorrhizae and usually form bacterial nodules. The members of the third subfamily, Caesalpinioideae, rarely form nodules, and one of the included groups, the two large, pantropical, closely related tribes Amherstieae and Detarieae, regularly form ectomycorrhizae. Nodules and ectomycorrhizae may well be alternative means of supplying organic nitrogen to the plants that form them.

Those plants having endomycorrhizae usually occur in forests of high species richness, whereas those with ectomycorrhizae usually occur in forests of low species richness. The roots of ectomycorrhizal trees, however, support a large species richness of fungal symbionts, probably amounting to more than 5000 species worldwide, whereas those of endomycorrhizal trees have low fungal species richness, with only about 30 species of fungi known to be involved worldwide. Ectomycorrhizal forests are generally temperate or occur on infertile soils in the tropics. They apparently have expanded in a series of ecologically important events through the course of time from the Middle Cretaceous onward at the expense of endomycorrhizal forests.

The invasion of the land by the ancestor of the vascular plants clearly seems to have been facilitated by the origin of symbiotic associations between these plants and certain "phycomycetous" fungi similar to those that are involved in endotrophic mycorrhizae at the present time (1–10). During the subsequent history of plants on land, additional kinds of fungus–plant associations have evolved in relation to the exploitation of different habitats and different population structures. The purpose of this paper is to review these associations in an ecological/evolutionary context and to explore the nature of the generalities that can be derived concerning them. Such relationships are particularly significant in view of the role of mycorrhizae in contributing to plant productivity and the consequent potential of manipulating such associations for human benefit (11). In pursuing the ecological and evolutionary patterns involved, we first review the characteristics of the different kinds of mycorrhizae.

KINDS OF MYCORRHIZAE

Endomycorrhiza. The fungus penetrates roots to form characteristic intracellular vesicles and arbuscles. Endomycorrhizae probably are regularly formed by about four-fifths of all vascular plants (12) including *Psilotopsida, Lycopsida,* ferns [such as mycothalli and mycorrhizomes (13)], gymnosperms, and angiosperms. They have actually been observed in some 200 families and more than 1000 genera (14). Endomycorrhizae are formed with about 30 morphospecies of "phycomycetous" fungi which are ubiquitous in distribution and physiologically unspecialized.

Ectomycorrhiza. The fungus does not penetrate living cells in the roots but, instead, only surrounds them. The extensive mycelium of ectomycorrhizal fungi extends out into the soil and may function in transferring nutrients directly from decaying leaves, especially in nutrient-poor tropical soils (15–18). With the exception of a doubtful record from *Pandanus* in Madagascar (19, 20), ectomycorrhizae are unknown in monocots. Among the gymnosperms, they are characteristic of Pinaceae and some Cupressaceae [*Cupressus, Juniperus,* and possibly *Chamaecyparis* (21)] as well as *Gnetum* (22, 23).

Among the dicots, ectotrophic mycorrhizae are probably characteristic of all members of Fagaceae, Betulaceae, Salicaceae, and Dipterocarpaceae subfamily Dipterocarpoideae. In addition, they are found in most Myrtaceae, in *Coccoloba* [Polygonaceae (21, 24, 25; D. P. Janos, personal communication)] and in *Neea* and *Pisonia* [Nyctaginaceae (23, 24, 26, 27)].

In the legumes, the members of the two large, closely related pantropical tribes Amherstieae and Detarieae of the subfamily Caesalpinioideae that have been examined are nearly always ectotrophic (22, 26–33). Trees of these tribes, which are abundant in the forests of Africa and South America, regularly form dense, often monospecific, stands, characteristically on infertile soils (34). The genera in which ectotrophic mycorrhizae have been reported so far include *Afzelia, Anthonontha, Brachystegia, Eperua, Gilbertiodendron, Intsia, Julbernardia, Macrolobium, Monopetalanthus,* and *Paramacrolobium.* Members of the other two subfamilies of legumes, Mimosoideae and Papilionoideae, regularly form bacterial root nodules and fix nitrogen. Such nodules are not regularly formed, however, in Caesalpinioideae except in the genera *Chamaecrista* and *Erythrophloeum* (35). Ectotrophic mycorrhizae may have the ability, lacking in higher plants, to absorb and utilize organic nitrogen (such as ammonium) taken directly from decaying organic matter (36, 37). It seems likely that they were an important factor in the early evolutionary radiation of the tribes Amherstieae and Detarieae which, in turn, as judged by their morphological relationships and evolutionary position among the legumes, were evidently the first group of the family to diversify greatly. Endotrophic mycorrhizae, which occur in nearly all legumes other than the tribes Amherstieae and Detarieae, may lack the enzymes necessary to obtain nitrogen from leaf litter.

Other reports of ectotrophic mycorrhizae in legumes are scattered and include those from *Inga* (24, 29) and introduced

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U. S. C. §1734 solely to indicate this fact.

Acacia in New Zealand (22), both Mimosoideae, and others from *Aldina* (27, 29) of the Papilionoideae and *Bauhinia* (30, 32) of the Caesalpinioideae. Another species of *Bauhinia*, and other caesalpinioid legumes (38; unpublished data), are reported to have only endotrophic mycorrhizae, but the situation should be investigated further. Of special interest are *Sclerolobium* and *Diptychandra*, caesalpinioid legumes of the tribe Caesalpineae that are transitional to the tribes Amherstieae and Detarieae. The third genus of the group, *Tachigalia*, forms endotrophic mycorrhizae (D. P. Janos, personal communication).

Other groups of dicots in which ectomycorrhizae have been recorded are listed below. Some of these records seem quite secure but others appear to refer to situations in which plants were growing in proximity to others that are obligately ectomycorrhizal. For example, this has been demonstrated by Cooper (39) for ferns growing under *Pinus* and *Nothofagus* and suggested by Pegler and Fiard (24) for *Inga* growing in dry, sandy conditions near ectotrophic *Pisonia*. Ectomycorrhizae have been reported to occur in Aceraceae [*Acer* (28)], Bignoniaceae [*Phyllarthron*, Madagascar (19, 20)], Combretaceae [*Terminalia*, New Guinea (22)], Euphorbiaceae [*Uapaca*, Madagascar (19, 20); Nigeria (33)], Juglandaceae [*Carya* (22); *Juglans* (28)], Rhamnaceae [*Pomaderris*, New Zealand (22); *Rhamnus* (40)], Rosaceae subfamily Pomoideae (28, 41) and *Prunus* (41), Rubiaceae [*Psychotria*, Brazil (27)], Sapindaceae (22, 42–45), Sapotaceae [*Glycoxylon*, Brazil (27)], Tiliaceae [*Tilia* (28)], and Ulmaceae [*Ulmus* (28)].

Ectomycorrhizae are mostly formed with basidiomycetes, but also some are formed with ascomycetes. These represent the most advanced groups of true fungi; they coevolved with plants on land and utilize a diet of complex organic substrates. Moser (46) estimated that there are about 2000 species of *Cortinarius;* as far as is known, all form ectomycorrhizae. If other ectomycorrhizal genera are considered (29), an estimate of 5000 mycobionts involved in ectomycorrhizal symbiosis is probably conservative.

The ectotrophic mycorrhizae associated with Pinaceae, *Cupressus*, *Juniperus*, Betulaceae, Fagaceae, and Salicaceae seem to have evolved largely with members of the order Agaricales and also seem to have been characteristic associates of the ancestors of *Nothofagus* (Fagaceae) before this genus or its ancestors reached the southern hemisphere. The same ectomycorrhizal biota became associated relatively early with the leguminous tribes Amherstieae and Detarieae, a group clearly linking Eurasia with Africa/South America (47, 48) and with other ectomycorrhizal groups in the tropics, especially in areas of very poor soil such as those discussed by Janzen (30). Perhaps the mycorrhizal biota associated with *Eucalyptus* and other Myrtaceae in the tropics and southern hemisphere spread there with *Nothofagus* or its ancestors. Dipterocarpoideae, on the other hand, may have entered into its mycorrhizal association independently, perhaps in the Asian tropics, and then this fungal biota may have spread to some of the already ectomycorrhizal north-temperate groups mentioned above. Among its mycorrhizal fungi, rough-spored boletes, which are generally characteristic of the warmer regions of the Old World, are particularly conspicuous. Dipterocarpaceae are also characterized by the absence of parasitic rust fungi (Uredinales), which have coevolved and diversified especially with the Pinaceae, Betulaceae, Salicaceae, legumes, and Rosaceae, and by a growth habit referred to by Richards (49) as "family dominance," in which a number of different members of the family growing together dominate a particular plant community. Dipterocarpaceae are known in the fossil record only from the Oligocene onward (50) and thus may be considerably younger than the other ectomycorrhizal groups of higher plants.

Ericaceous and Orchidaceous Mycorrhizae. The Ericaceae and their close relatives Diapensiaceae (51), Epacridaceae (52), and Empetraceae (51) are strongly mycotrophic, with the fungus constituting up to 80% of the mycorrhize by weight in heavily "infected" *Calluna* (53). Although this partnership is expensive in terms of energy, it may have permitted the Ericaceae to colonize poor, acidic soils.

In the "ericoid" type of mycorrhiza seen in Ericaceae tribes Ericeae, Vaccinieae, Rhododendreae, and Calluneae and in related families, the fungus is endophytic. In the "arbutoid" type found in members of Ericaceae tribe Arbuteae and subfamilies Pyroloideae and Monotropoideae, the association is ectendotrophic, the fungus growing within and also ensheathing the root tissue. The identity of the mycobionts is largely unknown, but both ascomycetes and basidiomycetes are involved.

Orchids are obligately mycotrophic; in nature their seeds will germinate only in the presence of suitable fungi (54). The orchidaceous mycorrhiza is unique because the endophytic fungus also supplies the plant with carbon at least during the orchid's heterotrophic seedling stage. The "host" fungi are often basidiomycetous Tulasnellales (54), an order that normally contains plant parasites and saprobes which are able to utilize complex carbon sources such as cellulose and, in some cases, even lignin (55, 56). Mature autotrophic orchid plants appear to be nonmycorrhizal.

FACULTATIVE MYCOTROPHISM AND THE NONMYCORRHIZAL CONDITION

These phenomena appear to be correlated with herbaceous habit, shortening of life cycle, and evolution of root systems with abundant root hairs (52, 57).

In an elegant study of mycotrophism in pteridophytes, Boullard (13) demonstrated progressive reduction, in extent and duration, of endotrophic symbiosis: from *obligate* and present in both gametophytic and sporophytic generations in Psilotopsida and some Lycopsida and eusporangiate ferns, to *facultative mycotrophism* (sometimes present only in the sporophyte) in other eusporangiate and most leptosporangiate ferns, especially Polypodiaceae and Vittariaceae, to *absent* in Isoetaceae and aquatic Azollaceae, Salvinaceae, Marsileaceae, and Parkeriaceae (of which, the first are known to harbor symbiotic nitrogen-fixing *Anabaena*). Interestingly, endotrophic symbiosis in *Equisetum* is very rare and, when present, atypical, although it was well represented in the Carboniferous arborescent progenitors of this genus.

Among flowering plants, the members of a few families form mycorrhizae rarely. These include aquatics and plants that normally grow in waterlogged soils (14, 42), as well as halophytes. Families of monocots in which mycotrophism is normally absent are the related Cyperaceae and Juncaceae (58) (but see Ref. 59). Among the dicots, all families of Centrospermae, including Caryophyllaceae, usually lack mycorrhizae (60–62). Polygonaceae are traditionally regarded as lacking mycorrhizae, (26, 60), but *Coccoloba* forms ectomycorrhizae (24, 26) and some species of *Eriogonum* (63) form endomycorrhizae. In these dicot groups, the loss of mycorrhizae is probably correlated with a weedy, herbaceous habit, and the woody members will probably be found to have either endotrophic or, more rarely, ectotrophic mycorrhizae when they are examined (63). Just such a pattern is starting to emerge for Chenopodiaceae (62–64).

Brassicaceae also usually lack mycorrhizae (59–62). In regard to the often woody family Capparaceae, from which Brassicaceae were derived, reports are mixed (38, 42). Perhaps all families that are rich in glucosinalates will be found predomi-

nantly to lack mycorrhizae, as already reported for the small family Resedaceae (60) but not yet investigated in Moringaceae, Salvadoraceae, and Tropaeolaceae. Such a relationship might have to do with the inhibitory action of chemical substances on fungal growth.

At least two genera of Nyctaginaceae, *Neea* (26, 27) and *Pisonia* (24), are ectomycorrhizal, at least in the American tropics. They are the only members of the otherwise nonmycorrhizal Centrospermae reported to form such associations, and ectomycorrhizal associations probably evolved independently in this groups of plants. Perhaps they, and *Coccoloba* as well, have acquired mycorrhizae, which might be of special importance in relation to their woody habit and frequent occurrence in relatively infertile soils.

Those families of angiosperms that lack mycorrhizae have fine roots abundantly provided with roothairs, as demonstrated by Baylis (52, 57). The distinctive, dense, brushlike roots of Proteaceae are especially notable in this respect, and Proteaceae are unique as a large family (more than 1000 species) of trees and shrubs that entirely lack mycorrhizae (65–67).

ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF MYCORRHIZAL SYMBIOSIS IN FOREST COMMUNITIES

In contrast to herbs, in which the occurrence and intensity of mycorrhizal symbiosis is more erratic, most trees and shrubs are strongly mycotrophic (33, 34, 68). As Trappe and Fogel (ref. 14, p. 205) pointed out, "Most woody plants require mycorrhizae to survive, and most herbaceous plants need them to thrive." The most prominent exceptions are Proteaceae, which are nonmycorrhizal, and cycads, whose association with the nitrogen-fixing blue-green alga *Anabaena* appears to be of great antiquity. As far as fungal symbiosis is concerned, again with the exception of Ericaceae and a few related families with their distinctive mycorrhizae, all other woody mycotrophic plants are either endo- or ectomycorrhizal. The pattern of the occurrence of these two basic types of mycorrhizae is discussed below.

Endotrophic Forests. The different fungal strains involved in endotrophic mycorrhizae are, in general, neither host specific nor geographically limited (52, 69, 70) although there may be local differences correlated with soil characteristics (71) and microbiota (72). If the association of a particular kind of plant with a particular kind of fungus is relatively constant, different individuals of this plant may be more likely to compete with one another directly than if they were involved with a wide variety of different fungi, as in situations involving ectotrophic mycorrhizae (73). This may in turn lead to relatively wide spacing of individuals in endotrophic communities and a high species diversity of the plants. The clumping of endomycorrhizal trees, when it occurs, may be linked with exceptional ecological circumstances, such as waterlogged soils (e.g., ref. 74).

Under tropical conditions, in which individuals of a given species of plant are often widely spaced and infrequent, the pattern of forming associations with a relatively few species of endotrophic fungi may be analogous with the situation reported for parasitoid insects (75) or bark beetles (76). In these groups, the host plants may simply be too rare to allow extreme specialization. In this sense, the lack of specialization paradoxically may be a property of certain kinds of rich (= diverse) communities. These two correlated phenomena, involving a lack of diversity on the part of the mycobionts and a high diversity in the phytobionts, are directly correlated and a general factor in determining the structure of the communities in which they occur.

The cultivation of endomycorrhizal trees in pure stands contradicts the high diversity patterns characteristic of natural endotrophic communities. Cultivation practices, especially in plantations of tropical trees, usually exploit methods such as interplanting that increase local diversity (77). Under tropical conditions, stands of endotrophic crops can be maintained, but at an unusually high cost in labor, fertilizer, and pesticides. The role of mycorrhizae in agricultural productivity should be studied more intensively than at present to find ways to increase crop yield that are not expensive in energy (14).

Ectotrophic Forests. In ectotrophic forests, the mycobionts are very diverse and the phytobionts often form stands that are monotonous and uniform. In most cases, symbiosis is obligatory, as in endomycorrhizal associations, but the ectomycobiont is often specific to one or only a few kinds of phytobionts. The phytobionts themselves have the capacity of forming consortia with a wide range of mycobionts, usually simultaneously (12, 14), so that individuals occurring side by side may avoid direct competition with one another.

In native cool-temperate ectotrophic forests there are many fungi that can form mycorrhizae with members of the dominant species of trees (28). Zak (78) estimated that Douglas fir (*Pseudotsuga menziesii*) has about 100 species of fungi as potential ectomycorrhizal partners, of which some appear to be host specific and others can associate with members of other genera and families of plants. This estimate appears to be conservative: the corresponding estimate given by Trappe (12) is 2000.

Furthermore, ectomycorrhizal phytobionts appear to take up mycobionts selectively, according to developmental phase, ecological conditions, and, possibly, climatic fluctuations (28). Seedlings often have different mycobionts than established plants, and these mycobionts are replaced as the plant matures (79). In such communities, the diversity is below the ground, where various mycobionts on roots of the same species of phytobionts form symbiotic associations that may not compete directly with each other for the same nutrients at the same time. There is good evidence that symbiosis with a specific mycobiont can affect the physiology of the ectotroph—for example, by increasing its tolerance to high soil temperatures (80) or resistance to pathogens (81). As Trappe (ref. 12, p. 214) pointed out, "mycorrhizal fungi clearly differ between species and ecotypes in production of critical enzymes." Ectotrophic forests, of which boreal coniferous forests are the best known example, start on new sites with various phytobiont species but become increasingly dominated by one of them (82) to reach a state of equilibrium "which enables the best adapted species to form ectomycorrhizal forests of a relatively great stability" (ref. 28, p. 88). But this stability only pertains to the phytobionts in such forests. In endomycorrhizal forests the individual kinds of trees are often widely dispersed, whereas in ectomycorrhizal forests it is the mycorrhizal fungi that have a similar pattern of occurrence. At fruiting time, different combinations of mushrooms, varying from season to season, are found even under the same tree in a mosaic of mostly nonoverlapping distributions (83, 84).

Most forests in which single species of trees dominate are composed of ectotrophs; examples include forests dominated by caesalpinioid legumes of the tribes Amherstieae and Detarieae in the tropics (28, 30, 49), *Eucalyptus* in Australia, or Pinaceae in the northern hemisphere. The dense, "gregarious," species-poor stands of Fagaceae in Malesia were described especially well by Soepadmo (85). Dipterocarpaceae, which dominate both species-rich and species-poor habitats in the Asian tropics, evidently are all ectotrophic (29, 30, 33, 86–89). Where Dipterocarpaceae occur in species-rich forests on rela-

tively fertile latosols, they still dominate at a family level, several genera possibly sharing the same species of mycobionts as commonly happens in temperate ectomycorrhizal forests composed of different members of Fagaceae or Pinaceae.

DISCUSSION

Ectotrophic trees form extensive forests in areas, such as much of Eurasia and North America, that have been subjected to severe climatic stress in the past or that now experience strongly seasonal climatic conditions or have poor soils (90). For example, most of the endotrophic trees and shrubs that formed mixed forests over much of North America earlier in the Tertiary became extinct following the middle Pliocene episode of increasing aridity and are now confined to regions of equable climate such as coastal California and the southern Appalachians (e.g., ref. 91). Similarly, repeated periods of cooling during the late Cenozoic in Europe progressively reduced diversity of the rich mixed mesophytic forest in favor of the present-day ectotroph-dominated vegetation (92).

In apparently uniform ectotrophic forests, a diverse assemblage of mycobionts is characteristically present. This diversity contrasts with the situation in most diverse tropical forests, with their species-poor component of physiologically unspecialized endomycobionts. The ubiquity of endomycobionts seems to make the dispersal and establishment of their associated plants relatively simple, whereas the dispersal of the plants associated with ectomycobionts is apparently difficult, as in Fagaceae for example (93, 94). This may be because of the necessity of concomitant dispersal of both the seeds and the spores, or even of two kinds of compatible spores in the case of heterothallic ectomycobionts. Small mammals that eat the seeds and the ectotrophic fungi often may disperse both, but only locally (95). The fact that caesalpinioid legumes of the Amherstieae/Detarieae complex with ectotrophic mycorrhizae are found on both sides of the Atlantic (in Africa and South America) suggests that they did in fact cross sea gaps of at least 1000 km, since the main evolutionary radiation of the group is unlikely to have taken place before the Eocene (96). Anemophily and dry, unpalatable fruits have evolved mainly in the ectotrophic, species-poor forests of the northern hemisphere; entomophily and fleshy fruit enticing to widely foraging animals are more characteristic of endotrophic forests, where establishment is relatively likely following long-distance dispersal (97).

Historically, Pinaceae may have originated by the Late Triassic (98) and certainly existed in the Jurassic (99), with *Pinus* in existence at the start of the Cretaceous (100). The major differentiation of the family, however, took place from the Middle Cretaceous onward, when Betulaceae, Caesalpinioideae, Fagaceae, and Salicaceae originated (47, 50, 96). Dipterocarpoideae, with their distinctive mycobionts, are probably younger than the other groups, having a fossil record dating back only to the Oligocene (50). Ectomycorrhizal associations with these plants may first have evolved in the Late Cretaceous in relation to areas of infertile soils. The expansion of now dominant ectomycorrhizal groups seems to have often taken place at the expense of endomycorrhizal forests and to have been an important feature in the evolution of flowering plants as a whole.

In general, these are the trees that form the timberline forests (101) and cover vast areas in the northern parts of the northern hemisphere (102–104). With the exception of *Nothofagus* (Fagaceae) and a few species of *Alnus* and *Salix* that reached South America in the Quaternary, these families are absent from the southern hemisphere. There, the timberline is formed largely by *Nothofagus* (103, 105), another ectotrophic tree that is the only member of the Fagaceae in the southern hemisphere. If Pinaceae, Betulaceae, and Salicaceae had not evolved in the northern hemisphere, timberline there too would be formed by Fagaceae. Wardle (106) has pointed out the necessity of extensive mycorrhizal growth for the establishment of such trees as *Eucalyptus*, *Pinus*, and *Picea* near the timberline in New Zealand. He has also pointed out the absence of arborescent monocots in timberline situations (103); monocots lack ectotrophic mycorrhizae. Gregarious woody genera that form associations at and above the timberline but which are not known to form ectotrophic mycorrhizae should be examined for the existence of such associations. *Dendrosenecio* and arborescent *Lobelia* species in the mountains of East Africa and *Espeletia* and *Polylepis* in South America would seem to be prime candidates for investigation.

It does seem clear that ectotrophic mycorrhizae confer a selective advantage on their phytobionts. In turn, wind-pollination probably evolved in these families as a consequence of the fact that their ectotrophic condition made it possible for them to occur in pure or nearly pure stands in habitats marginal for most kinds of trees (107).

In the tropics also, ectotrophs are characteristic of marginal conditions, both at high elevations and on very poor soils (27, 30). In temperate regions, they have been noted also as efficient colonizers on black wastes from anthracite mining, where endotrophs do not survive (108). Clearly, ectomycorrhizal associations have selective value in extreme environments, perhaps from their direct role in breaking down leaf litter and more specialized and controlled recycling of nutrients to the plants concerned (16, 28, 109, 110). The mycobionts may have the ability, lacking in the phytobionts, to utilize organic nitrogen taken directly from decaying leaves or ammonia-rich soils (36). Janos (26) has suggested that clumping may be especially critical on nutrient-poor soils, because the fungi may fruit relatively rarely under such circumstances, and their dispersal may therefore be more limited than otherwise.

On the other hand, the mycobionts may constitute 35–45% of the dry weight of the ectomycorrhiza in contrast to perhaps only 10–15% of the endomycorrhiza, so that the ectomycorrhizal sheath is energy-expensive to the plant on which it occurs (109). Janzen (30) has argued persuasively that the leaves of plants growing on poor soils in the tropics, many of which are now known to be ectomycorrhizal, may be more regularly and strongly provided with toxic substances than other (endomycorrhizal) plants, thus gaining a degree of protection from herbivores. In addition, the ectomycorrhizal fungi may themselves secrete substances that inhibit other pathogenic fungi and thus serve to protect their hosts (81). The "defensive compounds" may also play a role in suppressing and keeping endotrophs in check (14), thereby helping ectotrophs to maintain a hold on territory that they win opportunistically. Although not competitive with endotrophs, ectotrophs behave like "woody weeds" in exploiting situations that weaken endomycorrhizal systems, such as extreme temperature fluctuations, fire (adaptations of certain pines to seasonal burning might be the case in point here), land slides, soil disturbance caused by man, and, on a large scale, glaciation.

We thank Drs. P. S. Ashton, D. L. Hawksworth, D. P. Janos, D. H. Janzen, C. Jeffrey, D. N. Pegler, R. M. Polhill, T. St. John, and R. H. Whittaker for reading various drafts of our manuscript and offering their valued criticisms, and Drs. G. T. S. Baylis, B. Boullard, E. Horak, D. P. Janos, and J. E. Rodman for helpful discussions of related matters.

1. Treub, M. (1884) *Ann. Jard. Bot. Buitenzorg* **4**, 107–138.
2. Treub, M. (1886) *Ann. Jard. Bot. Buitenzorg* **5**, 87–139.
3. Treub, M. (1888) *Ann. Jard. Bot. Buitenzorg* **7**, 141–150.
4. Treub, M. (1890) *Ann. Jard. Bot. Buitenzorg* **8**, 1–37.

5. Bernard, B. (1909) *Ann. Sci. Natl. Bot.* **9**, 1–196.
6. Church, A. H. (1921) *J. Bot. London* **59**, 7–13, 40–46.
7. Magrou, J. (1948) *Rev. Quest. Sci.* **1948**, 340–371.
8. Boullard, B. (1957) *Le Botaniste* **61**, 1–185.
9. Jeffrey, C. (1962) *Bot. Not.* **115**, 446–454.
10. Pirozynski, K. A. & Malloch, D. W. (1975) *BioSystems* **6**, 153–164.
11. Ruehle, J. L. & Marx, D. H. (1979) *Science* **206**, 419–422.
12. Trappe, J. M. (1977) *Rev. Phytopathol.* **15**, 203–222.
13. Boullard, B. (1979) *Syllogeus* **19**, 1–58.
14. Trappe, J. M. & Fogel, R. C. (1977) *Range Science Department Science Series* (Colorado State Univ., Fort Collins, CO), Vol. 26, pp. 205–214.
15. Stark, N. (1971) *Trop. Ecol.* **12**, 177–201.
16. Harrera, R., Merida, T., Stark, N. & Jordan, C. F. (1978) *Naturwissenschaften* **65**, 208.
17. Went, F. W. & Stark, N. (1968) *BioScience* **18**, 1035–1038.
18. Meyer, F. H. (1974) *Annu. Rev. Plant Physiol.* **25**, 567–586.
19. Heim, R. (1937) *Les Lactario-Russulés de domain oriental de Madagascar* (Lab. Crypt. Mus. Nat. Hist. Nat., Paris), Vol. 1, pp. 1–196.
20. Bouriquet, G. (1947) *Bull. Acad. Malgache* **25**, 12–23.
21. Levisohn, I. (1954) *Forestry* **27**, 145–146.
22. Horak, E. (1977) in *Proceedings of the Second International Mycology Congress*, Miami, FL (Int. Mycological Congress, Amherst, MA), Vol. 1, p. 305 (abstr.).
23. St. John, T. (1979) *Acta Amazonica*, in press.
24. Pegler, D. N. & Fiard, J. P. (1979) *Kew Bull.* **33**, Pl. 10, 601–628.
25. Kreisel, H. (1971) *Biol. Rundsch.* **9**, 97–98.
26. Janos, D. P. (1980) *Biotropica* **12**, in press.
27. Singer, R. (1978) *Persoonia* **9**, 421–438.
28. Meyer, F. H. (1973) in *Ectomycorrhizae, Their Ecology and Physiology*, eds. Marks, G. C. & Kozlowski, T. T. (Academic, New York), pp. 79–105.
29. Singer, R. (1975) *The Agaricales in Modern Taxonomy* (Cramer, Vaduz, Liechtenstein).
30. Janzen, D. H. (1974) *Biotropica* **6**, 69–103.
31. Tupas, G. L. & Sajise, P. E. (1977) *Kalikasan Philipp. J. Biol.* **6**, 229–244.
32. Redhead, J. F. (1974) *Plant Soil* **41**, 707.
33. Redhead, J. F. (1978) in *Tropical Mycorrhizae*, Provisional Report (International Foundation for Science, Stockholm), Vol. 1, pp. 121–133.
34. Janzen, D. H. (1979) in *Advances in Legume Systematics*, eds. Polhill, R. & Raven, P. H. (Royal Botanic Gardens, Kew, England), in press.
35. Corby, H. D. L. (1979) in *Advances in Legume Systematics*, eds. Polhill, R. & Raven, P. H. (Royal Botanic Gardens, Kew, England), in press.
36. Lewis, D. H. (1973) in *Taxonomy and Ecology*, ed. Heywood, V. H. (Academic, London), pp. 151–171.
37. Raven, J. A., Smith, S. E. & Smith, F. A. (1979) *Trans. Bot. Soc. Edinburgh* **43**, 27–35.
38. Maeda, M. (1954) *Kumamota J. Sci. Biol.* **3**, 57–84.
39. Cooper, K. M. (1976) *N. Z. J. Bot.* **14**, 169–181.
40. Laiho, O. (1970) *Acta For. Fenn.* **106**, 1–72.
41. Stahl, E. (1900) *Jahrb. Wiss. Bot.* **34**, 539–668.
42. Black, R. (1978) in *Tropical Mycorrhizae*, Provisional Report (International Foundation for Science, Stockholm), Vol. 1, pp. 73–86.
43. Singer, R. & Morello, J. H. (1960) *Ecology* **41**, 549–550.
44. Singer, R. & Digilio, A. P. L. (1957) *Lilloa* **28**, 247–268.
45. Singer, R. & Digilio, A. P. L. (1960) *Lilloa* **30**, 141–164.
46. Moser, M. (1968) *Acta Mycol.* **4**, 199–203.
47. Raven, P. H. & Axelrod, D. I. (1974) *Ann. Mo. Bot. Gard.* **61**, 539–673.
48. Raven, P. H. (1979) in *Tropical Botany*, eds. Larsen, K. & Holm-Nielsen, L. B. (Academic, London), pp. 1–24.
49. Richard, P. W. (1966) *The Tropical Rain Forest* (Cambridge Univ. Press, Cambridge, England).
50. Muller, J. (1970) *Biol. Rev. Cambridge Philos. Soc.* **45**, 417–450.
51. Asai, T. (1934) *Jpn. J. Bot.* **7**, 107–150.
52. Baylis, G. T. S. (1975) in *Endomycorrhizas*, eds. Sanders, F. E., Mosse, B. & Tinker, P. T. (Academic, London), pp. 373–389.
53. Read, D. H. & Stribley, D. P. (1975) in *Endomycorrhizas*, eds. Sanders, F. E., Mosse, B. & Tinker, P. T. (Academic, London), pp. 105–117.
54. Warcup, J. H. (1975) in *Endomycorrhizas*, eds. Sanders, F. E., Mosse, B. & Tinker, P. T. (Academic, London), pp. 85–104.
55. Lewis, D. H. (1975) in *Endomycorrhizas*, eds. Sanders, F. E., Mosse, B. & Tinker, P. T. (Academic, London), pp. 119–148.
56. Purves, S. & Hadley, G. (1975) in *Endomycorrhizas*, eds. Sanders, F. E., Mosse, B. & Tinker, P. T. (Academic, London), pp. 175–194.
57. Baylis, G. T. S. (1972) *Search* **3**, 257–258.
58. Powell, C. L. (1975) *Plant Soil* **42**, 481–484.
59. Read, D. J., Koucheki, H. K. & Hodgson, J. (1976) *New Phytol.* **77**, 641–653.
60. Gerdemann, J. W. (1968) *Annu. Rev. Phytopathol.* **6**, 397–418.
61. Hirrel, M. C., Mehravaran, H. & Gerdemann, J. W. (1978) *Can. J. Bot.* **56**, 2813–2817.
62. Moose, B. (1978) in *Tropical Mycorrhizae*, Provisional Report, (International Foundation for Science, Stockholm), Vol. 1, pp. 389–396.
63. Reeves, F. B., Wagner, D., Moorman, T. & Kiel, J. (1978) *Am. J. Bot.* **66**, 6–13.
64. Miller, R. M. (1979) *Can. J. Bot.* **57**, 619–623.
65. Purnell, H. M. (1960) *Aust. J. Bot.* **8**, 38–50.
66. Lamont, B. (1977) *Aust. Plants* **9**, 161–164.
67. Malajczuk, N. & Bowen, G. D. (1974) *Nature (London)* **251**, 316–317.
68. Redhead, J. F. (1968) *Trans. Brit. Mycol. Soc.* **51**, 377–387.
69. Janos, D. P. (1975) in *Endomycorrhizas*, eds. Sanders, F. E., Moose, B. & Tinker, P. B. (Academic, London), pp. 437–446.
70. Tinker, P. B. H. (1975) in *Symbioses*, eds. Jenkins, D. H. & Lee, D. L. (Cambridge Univ. Press, Cambridge, England), pp. 325–349.
71. Kruckelmann, H. W. (1975) in *Endomycorrhizas*, eds. Sanders, F. E., Mosse, B. & Tinker, P. T. (Academic, London).
72. Mosse, B. (1975) in *Endomycorrhizas*, eds. Sanders, F. E., Mosse, B. & Tinker, P. T. (Academic, London).
73. Whittaker, R. H. & Levin, S. A. (1977) *Theor. Popul. Biol.* **12**, 117–139.
74. Janzen, D. H. (1978) *Brenesia*, 14–15; 305–309.
75. Janzen, D. H. (1976) in *Proceedings 15th International Congress Entomology* (Entomological Society of America, College Park, MD), pp. 84–94.
76. Beaver, R. A. (1979) *Nature (London)* **281**, 139–141.
77. Waidynantha, U. P. de S. (1978) in *Tropical Mycorrhizae*, Provisional Report (International Foundation for Science, Stockholm), Vol. 1, pp. 419–424.
78. Zak, B. (1973) in *Ectomycorrhizae, Their Ecology and Physiology*, eds. Marks, G. C. & Kozlowski, T. T. (Academic, New York), pp. 43–78.
79. Bowen, G. D. & Theodorou, C. (1973) in *Ectomycorrhizae, Their Ecology and Physiology*, eds. Marks, G. C. & Kozlowski, T. T. (Academic, New York), pp. 107–150.
80. Marx, D. H. & Brian, W. C. (1975) *For. Sci.* **21**, 245–254.
81. Marx, D. H. (1972) *Annu. Rev. Phytopathol.* **10**, 429–454.
82. Shafi, M. I. & Yarranton, G. A. (1973) *Ecology* **54**, 897–902.
83. Ogawa, M. (1977) *Trans. Mycol. Soc. Japan* **18**, 1–19.
84. Ogawa, M. (1977) *Bull. Gov. For. Exp. Sta. Tokyo* **297**, 59–104.
85. Soepadmo, E. (1972) *Flora Malesiana Ser. I Spermatophyta* **7**, 268–270.
86. Singh, K. G. (1966) *Malay. For.* **39**, 1–319.
87. Horak, E. (1977) *Kew Bull.* **31**, 645–652.
88. Corner, E. J. H. (1972) *Boletus in Malaysia* (Govt. Printing Office, Singapore, Malaysia).
89. Alwis, D. P., de & Abeynayake, K. (1978) in *Tropical Mycorrhizae*, Provisional Report (International Foundation for Science, Stockholm), Vol. 1, pp. 135–148.

90. Moser, M. (1967) *Mitt. Forstl. Bundes Versuchanst. Wien* **75**, 357–380.
91. Axelrod, D. I. (1958) *Bot. Rev.* **24**, 433–509.
92. Hammen, T., van der, Wijmstra, T. A. & Zagwinj, W. H. (1971) in *The Late Cenozoic Glacial Ages*, ed. Turekian, K. K. (Yale Univ. Press, New Haven, CT), pp. 391–424.
93. Steenis, C. G. G., van (1971) in *Taxonomy, Phytogeography and Evolution*, ed. Valentine, D. H. (Academic, New York), pp. 275–288.
94. Cracraft, J. (1975) *Ann. Mo. Bot. Gard.* **62**, 227–250.
95. Trappe, J. M. & Maser, C. (1977) in *Mushrooms and Man*, ed. Walters, T. (Linn-Benton Community College, Albany, OR), pp. 165–177.
96. Polhill, R. M. & Raven, P. H., eds. (1980) *Advances in Legume Systematics* (Royal Botanic Gardens, Kew, England), in press.
97. Regal, P. J. (1977) *Science* **196**, 622–629.
98. Delevoryas, T. & Hope, R. C. (1973) *Am. J. Bot.* **60**, 810–818.
99. Harris, T. M. (1979) *The Yorkshire Jurassic Flora. V. Coniferales* [British Museum (Natural History), London].
100. Miller, C. N. (1977) *Bot. Rev.* **43**, 217–280.
101. Moser, M. (1967) *Mitt. Forstl. Bundes Versuchanst. Wien* **75**, 357–380.
102. Tranquilini, W. (1979) *Physiological Ecology of the Alpine Timberline* (Springer, Berlin), pp. 36–38.
103. Wardle, P. (1974) in *Arctic and Alpine Environments*, eds. Berry, J. D. & Berry, R. D. (Methuen, London), pp. 371–402.
104. Moser, M. (1966) *Allg. Forstztg.* **77**, 120–217.
105. Wardle, J. (1970) *N. Z. J. Bot.* **8**, 494–646.
106. Wardle, P. (1971) *N. Z. J. Bot.* **9**, 371–402.
107. Heinrich, B. & Raven, P. H. (1972) *Science* **166**, 597–602.
108. Schramm, J. R. (1966) *Trans. Am. Philos. Soc.* **56**, 1–194.
109. Harley, J. L. (1975) in *Endomycorrhizas*, eds. Sanders, F. E., Mosse, B. & Tinker, P. T. (Academic, London), pp. 1–24.
110. Slankis, V. (1973) in *Ectomycorrhizae, Their Ecology and Physiology*, eds. Marks, G. C. & Kozlowski, T. T. (Academic, New York), pp. 231–298.