Commentary

Ecto- or arbuscular mycorrhizas – which are best?

Few topics in ecology are as intriguing or bedeviling as comparative studies of different types of mycorrhizas formed in the same plant species. Attempts to determine the relative benefits from each fungal type to the host plant are fraught with difficulties (Jones *et al.*, 1998), and for this reason plants that form tripartite associations with arbuscular and ectomycorrhizal fungi make ideal experimental systems. Just such a tripartite system is explored in a report in this issue by Chen *et al.* (pp. 545–556).

Why compare mycorrhizas? Although both ecto- and arbuscular mycorrhizas are generally known to increase the uptake of nutrients such as phosphorus and nitrogen in infertile soils, their functions and the benefits they provide to their host plants may not be equivalent (Jones *et al.*, 1998). Hence the ecological benefits of the two types of symbiosis are of great interest to plant community ecologists and researchers studying nutrient cycling. Arbuscular mycorrhizas are formed as a symbiosis of plant roots with primitive fungi of the order Glomales (Zygomycetes), while ectomycorrhizas are formed with higher basidiomycetes and a few ascomycetes. Only a few plant genera and species are capable of forming both types of association, sometimes on the same root tip (Fig. 1), but it is these that are so useful in comparative studies.

> *'The data provide the first integrated, comparative view of the multiple mechanisms of interference by ectomycorrhizal fungi'*

Interactions among fungi inhabiting the same root system

Succession within a root system from predominantly arbuscular mycorrhizas to dominance by ectomycorrhizas has previously been noted in the Salicaceae and Myrtaceae in both field observations (Bellei *et al.*, 1992; Dominik, 1956; Gardner & Malajczuk, 1988; Lodge & Wentworth, 1990) and glasshouse experiments (Lapeyrie & Chilvers, 1985; Chen *et al.*, 1998). Some researchers studying the ecology of predominantly ectomycorrhizal plant species have questioned whether interference between the fungi is involved in succession from arbuscular to ectomycorrhizas. However, such successional replacement and negative associations are apparently only observed in plant species that are capable of sustaining high rates of colonization by either fungal type. Several mechanisms have previously been proposed to explain how ectomycorrhizal fungi might replace arbuscular mycorrhizal fungi in tripartite associations, including mechanical barriers posed by the ectomycorrhizal sheath (Chilvers *et al.*, 1987), chemicals of fungal or host origin, competition for root carbohydrates and effects on rhizosphere communities (Lodge & Wentworth, 1990).

One of the remarkable results of the study reported here by Chen *et al.* is that with a thoughtful, complete randomized block experimental design they were able to show that several different mechanisms were involved in successional replacement. The results show that reduction in arbuscular mycorrhizal root colonization in *Eucalyptus* was most severe when the ectomycorrhizal fungus *Laccaria* was present. Ectomycorrhizal fungal sheaths spread rapidly once the organism is established and may block access to new root tips by arbuscular mycorrhizal fungi (see also Chilvers *et al.*, 1987; Chilvers & Gust, 1982). A unique finding that Chen *et al.* have made, however, is that ectomycorrhizal fungi may have a greater impact on colonization by arbuscular mycorrhizal fungi by causing their host to reduce production of fine roots, thereby limiting the availability of new roots to the fungus. Although the results indicate that competition and/or interference by the ectomycorrhizal fungus has the most pronounced influence on succession, they also found that arbuscular mycorrhizal colonization decreased somewhat through time even in the absence of ectomycorrhizas, presumably as a result of physiological changes in the host plant receptivity to colonization with seedling age.

Importance for forest ecology and forestry

Chen *et al.* found that high growth rates were attained with ectomycorrhizas in both species of *Eucalyptus* tested, while results from arbuscular mycorrhizal fungi were variable. These data suggest the importance of inoculating *Eucalyptus* seedlings that are outplanted in sites lacking in abundant ectomycorrhizal inoculum. Previously, C. Davey (pers. commun.) noted that uninoculated *Eucalyptus* seedlings that were outplanted in South American llanos, where arbuscular mycorrhizal fungi are abundant but native ectomycorrhizal fungi are lacking, resulted in very poor growth except where ectomycorrhizal fungi were accidentally introduced from inoculated pines in a neighboring plantation.

The results with the *Eucalyptus* seedlings inoculated with both mycorrhiza types match those of previous studies showing that ectomycorrhizal fungi colonize roots more slowly than arbuscular mycorrhizal fungi (Chilvers *et al.*, 1987) unless there are nearby trees supplying carbon to the ectomycorrhizal fungi (Fleming, 1983). The results furthermore support the hypothesis of Dominik (1956) that arbuscular mycorrhizal fungi may be especially

Fig. 1. A dual ecto- and arbuscular mycorrhiza in *Populus deltoides*. The hyphae of the fungi are bright white. The ectomycorrhizal fungus is visible in the mantle covering the mycorrhiza tip and the Hartig net between the apical host-root cortex cells. The large-diameter hypha on the surface near the base of the mycorrhiza belongs to an arbuscular mycorrhizal fungus, and the white area below the ectomycorhizal mantle nearby contains arbuscles (highly branched, intracellular hyphae for nutrient exchange) of the arbuscular mycorrhizal fungus. The rounded bright structures elsewhere in the cortex are spores and vesicles (storage structures) of the arbuscular endomycorrhizal fungus.

important in seedling establishment of colonizing plant species that are also hosts for ectomycorrhizal fungi. Although ectomycorrhizas have previously been shown to stimulate growth of *Eucalyptus* in infertile soils, reports of arbuscular mycorrhizal effects on *Eucalyptus* have been ambiguous (Jasper & Davy, 1993; Adjoud *et al*., 1996). Through careful experimental design involving two *Eucalyptus* species (*E. globulus* and *E. urophylla*), two levels of P and three selected arbuscular mycorrhizal fungi for inoculum, Chen *et al*. stimulated the greatest growth rates in *E. globulus* in the low P treatment when it was inoculated both with the ectomycorrhizal fungus *Laccaria* and arbuscular mycorrhizal fungi. These results suggest that the additive beneficial effects from insuring simultaneous colonization by the two types of fungi could be useful for the establishment of commercial timber species in adverse sites. Commercially important trees that form tripartite associations include *Eucalyptus*, *Acacia*, *Casuarina* and *Populus* (Brundrett *et al*., 1996).

In contrast to the results with *E. globulus*, arbuscular mycorrhizal fungi did not confer any additional growth benefits to *E. urophylla* plants colonized by the ectomycorrhizal fungus *Laccaria*. In *E. urophylla*, however, one arbuscular mycorrhizal fungus (an *Acaulospora* strain) produced a growth response nearly equal to that of *Laccaria* when inoculated alone, while the other two arbuscular types stimulated growth to a much lesser extent. These results show that careful matching of host and fungal species (and genotype) are needed to obtain the best results.

Summary

The data reported by Chen *et al*. in this issue provide the first integrated, comparative view of the multiple mechanisms of interference by ectomycorrhizal fungi, together with innate changes in host plant physiology with age that are responsible for succession from arbuscular- to ectomycorrhizal dominant symbiosis in plants that form both types of mycorrhizas. Their results also underscore the complexities involved in tripartite mycorrhizal systems, including the variable responses to different host and fungal species combinations. Thus, while ectomycorrhizal fungi generally produced a high growth rate response in both species of *Eucalyptus* tested, results from one set of experiments cannot necessarily be used to predict the response of a different set of interacting plant and fungal symbionts.

D. J. Lodge

Center for Forest Mycology Research, USDA Forest Service, Forest Products Lab, Luquillo, PR 00773–1377, USA (tel +1 809 888 3801; fax +1 787889 7477; e-mail djlodge@coqui.net).

ACKNOWLEDGEMENTS

The Forest Products Lab in Wisconsin is maintained in cooperation with the University of Wisconsin, while the lab in Puerto Rico is maintained in cooperation with the USDA-Forest Service International Institute for Tropical Forestry. This Commentary was written by a US Government Employee on official time, and it is therefore in the public domain and not subject to copyright.

REFERENCES

Adjoud D, Plenchette C, Halli-Hargas R. 1996. Response of 11 *Eucalyptus* species to inoculation with three arbuscular mycorrhizal fungi. *Mycorrhiza* **6**: 129–135.

Bellei MM, Garbaye J, Gil M. 1992. Mycorrhizal succession in young *Eucalyptus viminalis* plantations in Santa Catarina (south Brazil). *Forest Ecology and Management* **54**: 205–213.

Brundrett M, Bougher N, Dell B, Grove T, Malajczuk N. 1996. *Working with mycorrhizas in forestry and agriculture*. ACIAR Monograph 32. Canberra, Australia: ACIAR.

Chen YL, Gong MQ, Wang FZ, Chen Y, Brundrett M, Dell B. 1998. Growth promotion and nutrient uptake of *Eucalyptus urophylla* co-inoculated with *Glomus* and *Pisolithus* isolates. In: Kakkiwa J, ed. *Proceedings of BIO-REFOR'97 workshop on rehabilitation of tropical forests*. Queensland, Australia: 153–155.

Chen YL, Brundrett MC, Dell B. 2000. Effects of ectomycorrhizas and vesicular-arbuscular mycorrhizas, alone and in competition, on root colonization and growth of *Eucalyptus globulus* and *E. urophylla*. *New Phytologist* **146**: 545–556.

Chilvers GA, Gust LW. 1982. Comparisons between the growth rates of mycorrhizas, uninfected roots and a mycorrhizal fungus of *Eucalyptus st-johnii* R. T. Bak. *New Phytologist* **91**: 453–466.

Chilvers GA, Lapeyrie FF, Horan DP. 1987. Ectomycorrhizal vs endomycorrhizal fungi within the same root system. *New Phytologist* **107**: 441–448.

Dominik T. 1956. Mycotrophy of poplars in their natural associations in Poland. *Roczniki Nauk Lešnych* **14**: 247–266.

Fleming LV. 1983. Succession of mycorrhizal fungi on birch: infection of seedlings planted around mature trees. *Plant & Soil* **71**: 263–267.

Gardner JH, Malajczuk N. 1988. Recolonisation of rehabilitated bauxite mine sites in Western Australia by mycorrhizal fungi. *Forest Ecology and Management* **24**: 27–42.

Jasper DA, Davy JA. 1993. Root characteristics of native plant species in relation to the benefit of mycorrhizal colonization for phosphorus uptake. In: Barrow HJ, ed. *Plant nutrition from genetic engineering to field practice*. Dordrect, The Netherlands: Kluwer Academic Publishers, 323–326.

Jones MD, Durall DM, Tinker PB. 1998. A comparison of arbuscular and ectomycorrhizal *Eucalyptus coccifera*: growth response, phosphorus uptake efficiency and external hyphal production. *New Phytologist* **140**: 125–134.

Lapeyrie FF, Chilvers GA. 1985. An endomycorrhiza–ectomycorrhiza succession associated with enhanced growth of *Eucalyptus dumosa* seedlings planted in a calcareous soil. *New Phytologist* **100**: 93–104.

Lodge DJ, Wentworth TR. 1990. Negative associations among VA-mycorrhizal fungi and some ectomycorrizal fungi inhabiting the same root system. *Oikos* **57**: 347–356.