Mycorrhizas: A context for species siting and management?

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Introduction

A mycorrhiza is an association between soil fungus and a plant root. Most vascular plants form mycorrhizal associations in which the fungus benefits from photosynthetically derived carbon compounds (Smith and Read 1997). In return, the plant gains the use of the fungal mycelium's very large surface area and small diameter that allows penetration of much finer soil pores than root hairs, to absorb water and mineral nutrients from the soil (Allen 1991). Additionally, mycorrhizal plants are often more resistant to diseases, such as those caused by microbial soil-borne pathogens.

Mycorrhizal types

Mycorrhizal associations are characterised by their morphology (Allen 1991, Brundrett *et al.* 1996, Marschener 1995). Several different types of mycorrhizas have been recognised but only two are important in New Zealand tree species, namely ectomycorrhizas (EM) and arbuscular mycorrhizas (AM). EM are characterized by the presence of a mantle of fungal hyphae[1] around the root surface, and hyphae that penetrate the spaces around root cortical cells, the Hartig net, which is the main site for nutrient exchange. In AM, the fungal hyphae penetrate host plant cells and develop structures called arbuscles and vesicles within the root cortical cells. Arbuscles are the main sites of nutrient exchange while vesicles (not present in all AM) are storage organs. Many EM fungi produce conspicuous fruiting bodies, some of which are well known (eg *Amanita, Boletus*), or are truffle-like and fruit beneath the soil surface (eg *Rhizopogon*). In contrast AM fungi produce inconspicuous fruiting bodies.

Mycorrhizas of important New Zealand exotic tree species

Many tree species from the northern hemisphere that have become important forest species in New Zealand, including all pines, Douglas fir and larch, form EM. The cypresses (macrocarpa, Mexican, Lawson and Leyland cypress) and redwood are important AM species. In species of some genera both EM and AM can occur together on the same tree root system - the proportions present may depend on factors such as the soil water content and soil aeration, or the age of the trees (Marschener 1995).

A list of exotic tree species important in New Zealand and their mycorrhizal type is given in Table 1. The list includes forest species (including species of minor importance), some common amenity (often forest species in other countries) and erosion control species as well as important forest weed species. It is notable that all of the forest weed species listed in Table 1 form AM; the mycorrhizal status of an additional species, Himalayan honeysuckle (*Leycestaria formosa*), has not been reported. Eucalypts, poplars, willows and acacias are examples of species that are reported to form dual mycorrhizas (EM and AM). In the Eucalypts there are reports that seedlings may initially form AM, but these are replaced by EM as they mature (Gardner and Malajczuk 1998), while the significance of EM species in acacias is controversial (Brundrett *et al.* 1996).

[1] A **hypha** *(plural* **hyphae***) is a long, branching filamentous fungal cell. A mass of hyphae is collectively called a mycelium.*

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Mycorrhizal type, tree nutrition and distribution

It has long been known that mycorrhizas enhance uptake of mineral nutrients, particularly of phosphorus. Research in the last 20-30 years has shown that mycorrhizas also play an important role in the uptake of nutrients from organic materials. Ericoid mycorrhizas (mycorrhizas associated with ericaceous species) and some EM species have the potential to degrade structural compounds of plant litter and mobilize nitrogen and phosphorus directly from organic polymers, so that they are able to short circuit the microbial mineralization process. This gives these species an advantage in environments where nitrogen and phosphorus

Figure 1. An AM species out of its comfort zone. Lawson cypress (Chamaecyparis lawsoniana) growing in a cool, upland environment near Lake Coleridge, Canterbury, showing yellowing characteristic of nitrogen deficiency, probably because of slow organic matter mineralization. An EM species, Douglas fir, is growing satisfactorily in the background and not showing deficiency symptoms.

Table 1. Mycorrhizal types of exotic forest, amenity and forest weed species. The list is compiled mainly from Harley and Harley (1987) and Brundrett et al. (1996).

Species forming ectomycorrhizas (EM)	Species forming arbuscular mycorrhizas (AM)	Species forming AM and EM
Forest species		
Pines (*Pinus* sp.)	Cypresses (*Cupressus* and *Chamaecyparis* sp.)	Eucalypts (*Eucalyptus* sp.)
Douglas fir (*Pseudotsuga menziesii*)	Coastal redwood (*Sequoia sempervirens*)	Poplars (*Populus* sp.)
Larches (*Larix* sp.)	Blackwood (*Acacia melanoxylon*)	
Amenity species		
Firs (*Abies* sp.)	Ash (*Fraxinus* sp.)	Willows (*Salix* sp.)
Spruces (*Picea* sp.)	Elms (*Ulmus* sp.)	Acacias (*Acacia* sp.)
Cedar (*Cedrus* sp.)	Walnut (*Juglans* sp.)	Alders (*Alnus* sp.)
European Beech (*Fagus sylvatica*)	Maples and sycamore (*Acer* sp.)	
Birches (*Betula* sp.)	*Prunus* sp.	
Chestnut (*Castanea* sp.)	Rowan (*Sorbus aucuparia*)	
Oak (*Quercus* sp.)		
Forest shrub weeds		
	Blackberry (*Ribes nigrum*)	
	Broom (*Cytisus scoparius*)	
	Gorse (*Ulex europeus*)	
	Pampas (*Cortaderia selloana*)	
	Buddleia[1] (*Buddleja davidii*)	

[1]Dickie *et al.* (2007).

mineralization rates are slow and the availability of these elements is limiting (see Read and Perez-Moreno 2003 for a review). Therefore EM species should perform relatively better than AM species under the cooler temperatures that occur at higher altitudes and latitudes or at other sites where nitrogen and phosphorus are limiting (Figure 1). Thus, the important AM species in New Zealand forestry, namely the cypresses, tend to be restricted to warmer, lower elevation sites and more fertile soils, hence they are commonly referred to as being "site demanding".

Most indigenous New Zealand forest species, including all the podocarps and most angiosperms, form AM. The exceptions are the beeches (*Nothofagus*) which form EM, and two species related to the eucalypts - kanuka (*Kunzea*) and manuka (*Leptospermum*), both of which, like the eucalypts, form AM as well as EM.

The role of mycorrhizas in the distribution of forest species seems evident in New Zealand indigenous forests as described by Peter Wardle (1964): "The beech species increase in abundance along environmental gradients that lead away from a moist, mild, fertile optimum" and subsequently by John Wardle (1984) in "The New Zealand Beeches" where he stated "……the beech forests are most prevalent at high altitudes, in the drier eastern and central regions of both main Islands, in the south, and on relatively infertile and poorly drained soils. They tend to give way to softwood/broadleaved-hardwood forest at low altitudes, in the moister western and coastal regions, to the north, and on better drained and more fertile soils. The environmental gradients most relevant to the distribution of beech forest are therefore those associated with changes in altitude, rainfall, latitude and soil conditions." From this, the natural distribution of the podocarp-broadleaved-hardwood (non-beech) species might be used to provide a template for the siting of exotic forest AM species in New Zealand.

All of the tree species that spread as wildings of any consequence in New Zealand form ectomycorrhizas (Hunter and Douglas 1984, Ledgard 2004). Ledgard (2004) lists eight species of pine, plus Douglas fir and larch as being the ten introduced species that contribute most of the wildings currently seen in New Zealand. The main locations where spread occurs in both the North and South Islands are upland (high country) environments. It seems likely that the ability of EM to mobilize nitrogen and phosphorus in these cool environments is an important factor allowing these species to establish and thrive there. All of the forest-weed species listed in Table 1 form arbuscular mycorrhizas. Three of these are confined to lowland environments, while two species - gorse and broom - occur in upland high country environments. It might be hypothesized that the ability of gorse and broom to grow in upland environments is due to the fact that both are efficient nitrogen-fixers. The arbuscular mycorrhizal habit and lack of ability to fix nitrogen suggests that buddleia, pampas and blackberry will not become major weeds in upland environments.

The type of mycorrhizal association is clearly not the only factor determining forest species distribution - numerous other factors such as tolerance to low temperature, out of season frost, drought, and ability to regenerate under forest canopies are also important. These factors, however, may be subordinate to mycorrhizal type in determining species distribution along climatic and soil fertility gradients.

Mycorrhizas and nutrition management

The nutritional differences between mycorrhizal types have implications for siting of species at local scales as well as the broad regional, latitudinal and altitudinal scales indicated above. Nutrient availability varies across landscapes, for example soils may be deeper and more fertile on lower slopes, in valley bottoms or at flush sites; these may be sites where the more 'site demanding' AM species are likely to be best located. Mycorrhizal differences also have implications for fertiliser management. A recent study that compared the growth of radiata pine (EM) and Mexican cypress (AM) at 35 sites across the New Zealand plantation forest estate showed that Mexican cypress responded more strongly to fertiliser than pine, the average volume responses of the two species at age two being 42 and 23% for cypress and pine respectively (Watt *et al.* 2005). These results indicate that the range of planting sites for AM species might be extended by fertiliser application. Similarly, although unknown, weed competition for nutrients may be particularly important for successful establishment of AM species at the nutritional limits of their range, hence attention to very good weed control may be important in extending the range of sites available for AM species.

While EM species may be better able to access nitrogen and phosphorus than AM species, the opposite may be true for the cations potassium, calcium and magnesium. In the study mentioned above, while Mexican cypress contained lower concentrations of nitrogen and phosphorus than radiata pine in the absence of fertiliser, it contained substantially higher cation concentrations, especially of calcium and magnesium (Davis *et al.* 2007). Magnesium is frequently deficient for radiata pine in New Zealand soils, but magnesium fertiliser application is often ineffective in correcting the deficiency (Beets *et al.* 2004). There may be situations where EM species are severely magnesium deficient but where AM species are capable of satisfactory growth and not affected by magnesium deficiency.

An intriguing possibility that remains to be explored is the potential of growing EM and AM species in mixtures to determine if this can be used to manipulate nutrient availability. The observations (Stone and Will 1965) of improved growth and nitrogen nutrition of AM species of *Araucaria* (in Australia), *Fraxinus* (in North America) and *Chamaecyparis* and *Cupressus* (in New Zealand) when planted adjacent to pines suggests EM species may enhance nitrogen uptake of AM species. In addition to mixtures of crop species such mixtures might include crop and understorey species. For example, can the nitrogen nutrition of an AM species (eg *C. lusitanica*, redwood) be improved and its site range extended by growing it in association with an EM species (eg Corsican pine (being slower growing and less competitive that radiata pine), manuka).

Mycorrhizas and nursery management

Trees require mycorrhizas for survival and growth in all but the moist fertile situations so it is essential that seedlings become mycorrhizal with appropriate species in the nursery or soon after planting. Severe chlorosis and poor growth of Douglas fir has been frequently reported in New Zealand, particularly in the South Island (Gilmore 1958), as a result of nursery stock lacking appropriate mycorrhizas. Gilmore (1958) found the problem could be corrected by puddling seedling roots in a clay:forest duff mixture before planting, or placing a handful of duff (the litter layer plus the upper 10 mm of mineral soil from a healthy 23-year-old Douglas fir forest) in the planting hole. Severe chlorosis in Douglas fir seedlings in Edendale nursery in 1981-1982 was found to be due to lack of appropriate mycorrhizas - seedlings were mycorrhizal but the fungal species present were ineffective (Chu-Chou and Grace 1987). The problem was corrected by inoculating seedlings in the bed with spores of an effective species (Rhizopogon parksii). These experiences indicate that new nurseries, nursery beds that have not had a recent crop of Douglas fir, and container-grown plants may need to be inoculated with mycorrhizal fungi, particularly if the above stress symptoms are observed in the nursery (or have been previously observed in seedlings after out-planting). Lack of mycorrhizas has not been reported to be a problem for pines or other exotic forest species in New Zealand, however it is possible that the complete failure of *Larix occidentalis* and poor early growth of *Abies* species in research trials may have been due to lack of appropriate mycorrhizae (C. Low, pers comm.).

Conclusions

An understanding of mycorrhizas at the level of mycorrhizal type (whether a species is AM or EM) may allow foresters to better site species and adjust fertiliser and herbicide usage to achieve better growth performance from the more site-demanding AM species, and perhaps extend their range. In time, research may show that there are advantages to be obtained from manipulation of mycorrhizal fungal species and growing species with different mycorrhizal types in mixtures to achieve nutrition benefits.

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