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Ericoid mycorrhizal association: ability to adapt to a broad range of habitats

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ABSTRACT

Ericoid mycorrhizal fungi are symbiotically associated with the roots of members of the Ericaceae which include genera such as *Calluna*, *Epacris*, *Erica*, *Rhododendron* and *Vaccinium*. These ericoid mycorrhizal associations have adapted to a broad range of habitats, from mor humus soils of the northern hemisphere to sandy soils occurring in the southern hemisphere. They also play an important part in enabling plants like *Calluna vulgaris* (L.) Hull in the northern hemisphere to colonize mine spoils which are inhospitable environments of toxic waste for growth of most plants. The mechanisms of utilizing complex forms of nitrogen and phosphorus and providing protection against toxic metals are described. These mechanisms carried out by ericoid mycorrhizal associations enable host plants to establish in diverse habitats.

1. Introduction

Mycorrhizal fungi are universally associated with root systems of plants but there are exceptions. The families Chenopodiaceae, Cruciferae and Resedaceae contain plants which show very poor or no mycorrhizal colonization (Smith & Read 1997). A mycorrhiza is an association of a fungus with root systems, in which both partners benefit from each other. There are two broad groups of mycorrhizas termed ectotrophic and endotrophic mycorrhizas and the latter are divided further into arbuscular, ericoid and orchidaceous mycorrhizas (Smith & Read 1997). In this paper, we concentrate on the ericoid mycorrhizal association and examine how the host plants in this association are able to establish and grow on a broad range of habitats.

2. Ericoid mycorrhizal fungi in the association

The fungi forming ericoid mycorrhizal associations are *Hymenoscyphus ericae* (Read) Korf & Kernan (Discomycetes, Ascomycotina), *Scytalidium vaccinii* Dalpé, Litten & Sigler (Deuteromycotina), *Cadophora finlandia* (Wang & Wilcox) Harrington & McNew (Deuteromycotina) and some *Oidiodendron* spp. (Deuteromycotina). Both *H. ericae* and *S. vaccinii* are very closely related (Egger & Sigler 1993) and *C. finlandia*, known as a dark septate endophyte, also belongs to the *H. ericae* aggregate (Vrålstad *et al.* 2000). The majority of these fungi can be cultured on artificial media. Although no conidia are formed by *H. ericae*, hyphae of *S. vaccinii* have been demonstrated to segment into a zig-zag formation as

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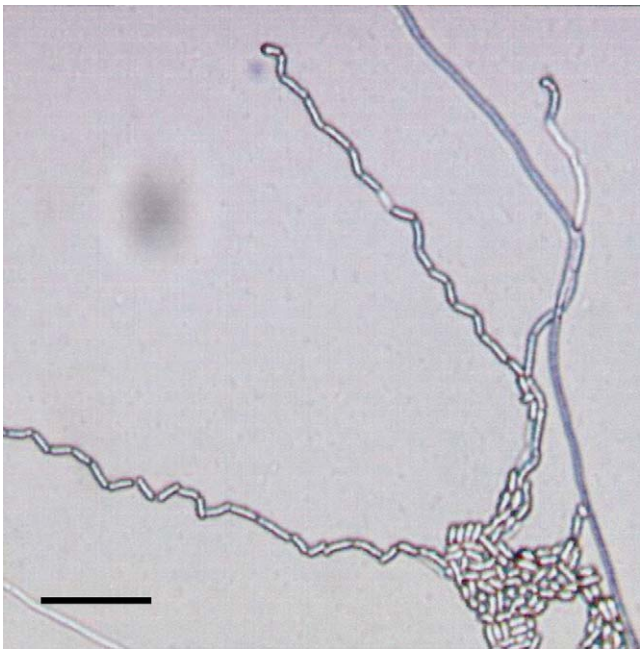

Fig. 1 – Segmenting hyphae of an ericoid mycorrhizal fungus forming arthroconidia, scale bar = 30 μm (Gibson 2004).

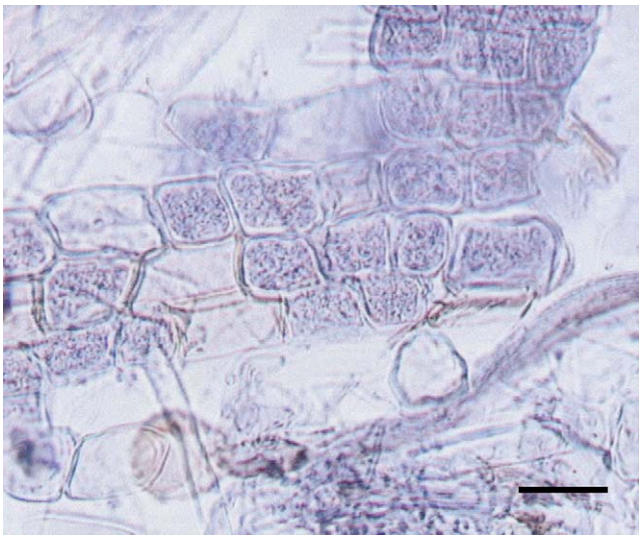

Fig. 2 – Cortical cells of 10-day-old cranberry colonized by an ericoid mycorrhizal fungus, scale bar = 30 μm (Gibson 2004).

arthroconidia-like structures (Pearson & Read 1973; Fig. 1). Small apothecia of *H. ericae* have been observed (Read 1974) confirming its identity within the Discomycetes. A number of different fungi have been isolated from the roots of *Epacris pulchella* Cav. in a south-eastern Australian sclerophyll forest and these isolates have been distinguished by DNA fingerprinting (Bougoure & Cairney 2005). This suggests that the populations of ericoid mycorrhizal fungi may be more diverse than was thought (Bougoure & Cairney 2005).

The hyphae of a highly infective fungus of *H. ericae* have numerous microfibrils projecting from the wall surface compared with sparse microfibrils found on the surface of a poorly infective isolate (Bonfante-Fasolo & Gianinazzi-Pearson 1982). These microfibrils are rich in polysaccharides and are supposed to anchor the fungus to the root as the first step in mycorrhizal colonization. The typical ericoid mycorrhiza consists of hyphal coils found in the cortical cells of thin roots, which have been termed hair roots (Fig. 2). The external mycelium extends no further than 1 cm from the surface of these hair roots. The ericoid mycorrhizal association is short lived, lasting no more than 11 weeks.

3. Distribution of ericoid mycorrhizal associations

Ericoid mycorrhizal associations are found in mor humus heathlands in the northern hemisphere (Fig. 3), Mediterranean woodlands, tropical cloud forests, the dry sand plains of Australia, Cape fynbos of South Africa and old copper mining sites of Ireland and the UK (Fig. 4). They appear to be confined to soils which are either peaty/highly organic or sandy, where the nutrients are low in availability (Read 1983). They are found in regions where the growing season is short and litter decomposition is slow. In the mor humus heathlands of the northern hemisphere, the limiting nutrient is primarily nitrogen, consisting of acid-hydrolysable organic compounds and insoluble humin, which are usually inaccessible to plants (Fig. 5; Stribley & Read 1974). The thin hair roots containing the ericoid mycorrhizas are found in the zone of decomposition beneath the litter layer. A typical heathland vegetation would consist of *C. vulgaris*, whose hair roots are confined to the top 10 cm of the soil, with other co-existing plants [*e.g. Molinia caerulea* (L.) Moench, *Eriophorum vaginatum* L. and *Deschampsia flexuosa* (L.) Trin.] having deeper rooting systems (Read 1996).

Ericoid mycorrhizal fungi have also been associated with ectomycorrhizas of conifer and deciduous trees in forests of north temperate and boreal zone, where *C. vulgaris* occurs as an understorey element (Bergero *et al.* 2000; Vrålstad *et al.* 2000). The fungus identified as *C. finlandia* produces black ectomycorrhizas named as *Piceirhiza bicolorata* in trees and also forms ericoid mycorrhizas in an ericaceous host, *Vaccinium*

Fig. 3 – A heathland site adjacent to Ticknock Forest, County Dublin, Ireland.

Fig. 4 – Natural revegetation of mine spoil by *Calluna vulgaris* and *Erica cinerea* at an old copper mine site at West Avoca, County Wicklow, Ireland.

myrtillus (Villarreal-Ruiz *et al.* 2004). However, the function and ecological significance of these mycorrhizal associations in north temperate forest communities have not yet been examined.

Old mining sites can be most inhospitable environments for the growth of plants (Fig. 4). In Ireland and UK, *C. vulgaris* and *Erica cinerea* L. are common on these sites which are polluted with metals (Bradley *et al.* 1982; Burt 1984). The survival of ericaceous plants on such sites indicates that transfer of metals to the plants is regulated by the ericoid mycorrhizal association and this will be discussed later.

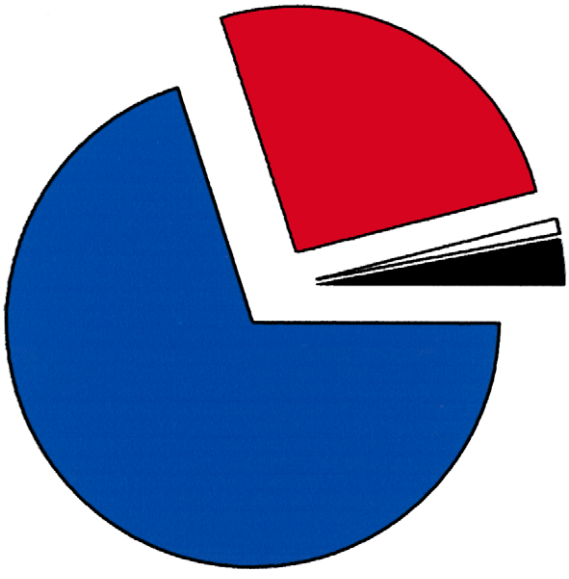

Fig. 5 – Proportion of different nitrogen fractions found in a peaty-gley soil, which is dominated by *Calluna vulgaris*. Blue section = hydrolysable organic-nitrogen, red section = proportion of humin and other recalcitrant nitrogen sources, black section = free amino acids and the white section = extractable ammonium-nitrogen (Kerley 1993).

4. Nitrogen nutrition of ericoid mycorrhizal associations

Acid heathland soils contain negligible amounts of available inorganic nitrogen due to slow decomposition rates (Fig. 5; Straker 1996; Haselwandter 1997). Plants belonging to the Ericaceae rely on ericoid mycorrhizal fungi to trap the broad range of different forms of nitrogen found in the soil. For example, cranberry plants (mycorrhizal and non-mycorrhizal) were grown in γ-irradiated soil amended with ^{15}N ammonium sulphate (Table 1; Stribley & Read 1974). Mycorrhizal plants were shown to have higher nitrogen contents but the proportion of ^{15}N to $^{14}N/^{15}N$ was greater in non-mycorrhizal plants (Table 1; Stribley & Read 1974). Their results revealed that ammonium-nitrogen was being utilized by non-mycorrhizal plants but mycorrhizal plants had access to other N sources within the soil as well as ammonium-nitrogen. The data indicated that the organic-nitrogen fraction of the soil was being used and that this was made possible by the presence of the ericoid mycorrhizal association. This work was continued by growing mycorrhizal and non-mycorrhizal plants in sand amended with nutrients containing a range of amino acids. Again mycorrhizal plants grew better and had higher total nitrogen contents than non-mycorrhizal plants (Stribley & Read 1980). In another experiment, *C. vulgaris* seedlings were inoculated with a range of ericoid mycorrhizal fungi and grown on nutrient agar in which the form of nitrogen was protein (Leake & Read 1991). The most effective inoculum for the growth of *C. vulgaris* was *H. ericae* and *S. vaccinii* (Leake & Read 1991). The least effective was the endophyte of *Rhodothamnus chamaecistus* (L.) Rchb., which occurs on base-rich soils and endophytes from two South African ericas occurring in the Cape sandy soils (Leake & Read 1991).

Ericoid mycorrhizal fungi have been shown to utilize a range of proteins as nitrogen and carbon sources (Bajwa & Read 1985) as well as other organic nitrogen sources such as chitin (Leake & Read 1990b; Kerley 1993). The ability of ericoid mycorrhizal fungi to utilize glutamine, ammonium or nitrate is affected by the availability of carbon in the growth medium (Grelet *et al.* 2005). When carbon supply was high, growth differences between strains were due to the total amount of

Table 1 – Nitrogen content and dry mass production of mycorrhizal and non-mycorrhizal cranberry seedlings after 6 months' incubation on soil [γ-irradiated and amended with N-15 $(NH_4)_2SO_4$]. * indicates significant differences between mycorrhizal and non-mycorrhizal (Stribley & Read 1974)

	Mycorrhizal	Non-mycorrhizal
Nitrogen concentration (% dry weight)	1.2	1.0
Dry mass production (mg)	30.3	21.0*
Total nitrogen (mg plant^{-1})	0.4	0.2*
N-15 excess (atom %)	15.4	20.0*

nitrogen taken up, suggesting variation in uptake kinetics (Grelet *et al.* 2005). Under carbon-limiting conditions, strain differences were related to nitrogen-use efficiency, indicating intraspecific differences in nitrogen metabolism between the different isolates (Grelet *et al.* 2005). Ammonium assimilation involves the reduction of ammonium ions to either glutamine by glutamine synthetase under low ammonium concentrations (*e.g.* <1 mM NH_4), or glutamate by glutamate dehydrogenase under high ammonium levels (Read *et al.* 1989).

Hymenoscyphus ericae has the ability to enzymatically degrade a number of complex nitrogen-containing compounds. Active polyphenol oxidases have been demonstrated during the release of organic nitrogen from recalcitrant compounds (Bending & Read 1996). The fungus also secretes an extra-cellular proteinase that cleaves protein to amino acids (Leake & Read 1989). This enzyme was identified as carboxyl (acid) proteinase of the pepsin type and showed optimal activity at pH 2.2, which is considerably lower than that found in acidic heathland soils (Leake & Read 1990a). However, the soil/litter interface, where most of the fine mycorrhizal roots of ericaceous plants are found, often shows a lower pH than the bulk soil due to the activity of H^+-releasing processes (Read *et al.* 1989). This interface is also the location where protein substrates accumulate. The proteinase activity of the fungus is, therefore, adapted to the specific micro-environment in which it is found. The low pH optimum of the proteinase may also protect the plant from protein degradation, as the pH within plant cells approaches neutral (Leake & Read 1989). It has been proposed that proteinase activity is regulated by a 'Noah's Ark' strategy, in which small quantities of enzyme are released as 'emissaries' in the absence of substrate (Leake & Read 1990c). When end products known as 'reporter' molecules are detected by *H. ericae*, this will lead to a rapid release of proteinase (Leake & Read 1990c). Excess proteinase is therefore only released by the fungus if suitable substrate is present in the soil. The end products or amino acids can be taken up directly by the ericoid mycorrhizal fungus without the necessity of them being deaminated further. These forms of nitrogen would also be ideal for transfer from the fungus to the host plant.

5. Phosphorus nutrition of ericoid mycorrhizal associations

Acid heathland soils contain negligible amounts of free inorganic phosphate and the main forms of phosphorus are organic, identified as phosphomonoesters, mainly phytates (Cosgrove 1967), or phosphodiesters such as nucleic acids (Griffiths & Caldwell 1992). Phytates are usually complexed with iron and aluminium and ericoid mycorrhizal fungi are able to access these sources (Mitchell & Read 1981).

A number of isolates have been shown to produce both extra-cellular and wall-bound phosphatases with wide substrate affinities (Straker & Mitchell 1986). All fractions contained a high molecular weight phosphatase (173K MW) with a broad pH optimum (2.0–6.0) but a smaller phosphatase (68K MW) with pH optimum at pH 6.5 was found in the wall fraction of low phosphate-fed mycelia. This study also demonstrated the hydrolysis of ATP, ADP and AMP by the low molecular weight phosphatase (Straker & Mitchell 1986).

While phosphomonoesters are quantitatively the most important fraction of organic soil phosphorus, utilization of phosphodiesters by ericoid mycorrhizal fungi has also received attention (Leake & Miles 1996; Myers & Leake 1996). Phosphodiesters are found in relatively low concentrations in most soils (usually <1 %) but are potentially valuable phosphorus sources (Griffiths & Caldwell 1992). Leake and Miles (1996) demonstrated the ability of *H. ericae* to degrade the phosphodiester DNA using extra-cellular and wall-bound phosphodiesterase. The phosphodiesterase released by the fungus had a pH optimum in the range of 4.0–5.5 but also showed a relatively high activity at lower pH levels (*i.e.* pH = 3.5). Leake and Miles (1996) also showed that nucleotides could be directly assimilated, suggesting that carbon and nitrogen could be taken up via this assimilatory route. This would enable phosphorus to be obtained by the fungus without the orthophosphate being precipitated with iron and aluminium, which can reach high concentrations in acidic heathland soils (Shaw & Read 1989). Further research revealed that cranberry seedlings mycorrhizal with *H. ericae* grew better than uninfected plants when grown on medium containing phosphorus as RNA or DNA (Myers & Leake 1996).

The kinetic properties for both phosphomonoesterase and phosphodiesterase have been determined and K_m and V_{max} were higher in the wall-bound fraction than in the extra-cellular and cytoplasmic fractions (Gibson & Mitchell 2005b). The addition of 0.25 mM copper to the growth medium did not affect wall-bound phosphatase activity of most isolates and stimulated extra-cellular phosphodiesterase of isolates from mine spoil sites but not those from uncontaminated sites (Gibson & Mitchell 2005b). A stimulation of phosphatases by copper may be interpreted as a metal avoidance mechanism, in which HPO_4 ions, released due to phosphatase activity, will react with metal ions (M^{2+}) to form insoluble $MHPO_4$ compounds (Gibson & Mitchell 2005b). This will thus result in immobilizing and detoxifying any free metal ions in the medium.

Few studies have considered the ability of these fungi to utilize phosphorus bound to sparingly-soluble, inorganic metal phosphates. Van Leerdam *et al.* (2001) investigated the phosphate solubilizing ability of a number of ericoid mycorrhizal fungi. When ammonium was present, most isolates were able to solubilize the rock phosphate hydroxyapatite. None of the isolates solubilized fluorapatite and hydroxyapatite when nitrate was added as the N source or when a pH buffer was added to the ammonium-containing medium. A number of isolates, mainly *Oidiodendron maius* Barron, were capable of solubilizing sparingly-soluble zinc phosphate in agar media (Martino *et al.* 2003). In another study using four *H. ericae*-type isolates, all were shown to solubilize zinc phosphate (Fig. 6) under varying nutrient conditions such as in the presence of different nitrogen forms and carbon concentration but only three of these isolates were able to solubilize calcium phosphate (Gibson & Mitchell 2004). None of the isolates solubilized aluminium, copper or iron phosphate. The dissolution of insoluble metal phosphates may take place by either protonation or chemical reaction with organic acids. Proton or organic acid release by fungi

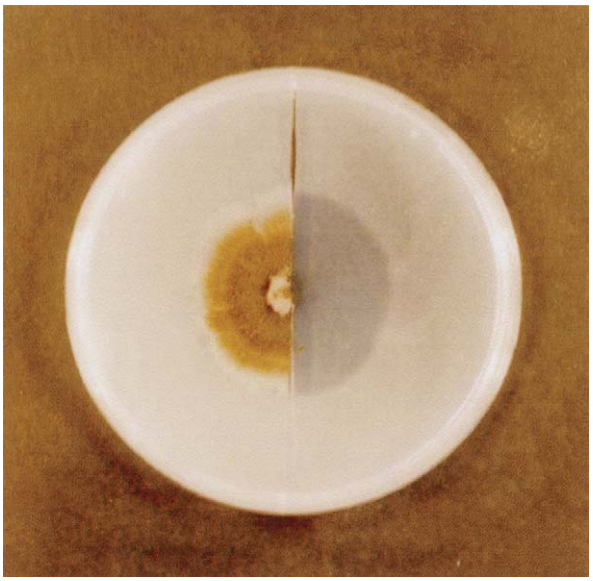

Fig. 6 – Growth of an ericoid mycorrhizal fungus on agar medium supplemented with zinc phosphate and alanine as the nitrogen source and overlain with cellophane which has been partly removed to reveal zone of solubilization (Gibson 2004).

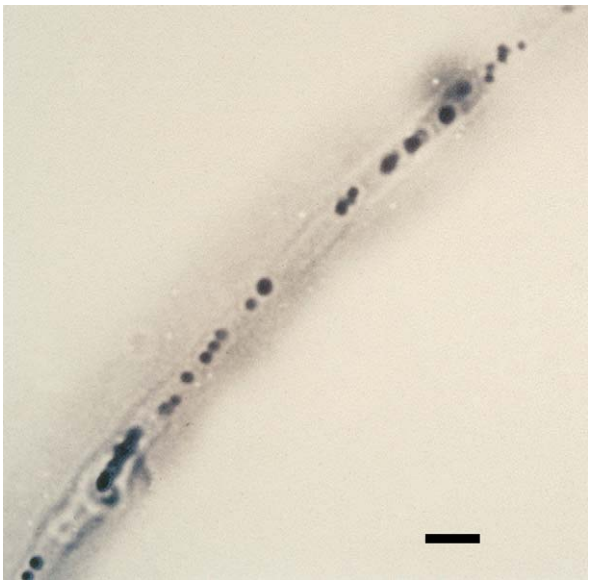

Fig. 7 – A hypha of an endophyte of *Rhododendron ponticum* stained with toluidine blue (pH 1.0) to show vacuolar granules of polyphosphate, scale bar = 5 μm (Straker 1986).

is influenced by the conditions and composition of the growth medium. For example, solubilization of iron-phosphate requires the involvement of siderophores, which are low molecular mass microbial compounds with a high affinity for iron (Winkelman 2002). Ericoid mycorrhizal fungi have been shown to produce siderophores but their biosynthesis decreases with increasing iron concentration (Dobernigg & Haselwandter 1992). While no iron phosphate was solubilized by the ericoid mycorrhizal fungi, this may have been due to the presence of iron-EDTA in the medium, which would have suppressed siderophore production (Gibson & Mitchell 2004).

The external hyphae, although no more than 1 cm from the root surface, act as extensions of the host root and thus function in the uptake of phosphate ions. There is evidence of movement of P-32 orthophosphate from the fungus to the plant (Pearson & Read 1973). Phosphate transport across membranes is carrier mediated and two uptake systems were identified in cultured mycelia of a South African isolate as high affinity and low affinity systems (Straker & Mitchell 1987). The uptake systems were shown to be sensitive to external pH with K_m increasing with a rise of pH. Although the high affinity system of the fungus was dominant at low P concentrations, the low affinity system played a significant role in uptake as well. Both P uptake systems operate better under the pH conditions typically found in the soils, such as the acidic mor humus soils of the northern hemisphere and the acidic sandy soils of the Cape, South Africa, where the ericoid mycorrhizal relationship occurs.

Under conditions of excess phosphate in the external medium, polyphosphate has been demonstrated to accumulate in the mycelium of ericoid mycorrhizal fungi (Straker & Mitchell 1985). Metachromatic granules (Fig. 7) accumulated during the lag phase of growth of these fungi and were related to the form and concentration of the external phosphorus source in the growth medium. These granules were located in the fungal vacuoles of both cultured and extra- and intra-cellular hyphae of naturally-occurring ericoid mycorrhizal root systems (Bonfante-Fasolo & Gianinazzi-Pearson 1981).

6. Ability of ericoid mycorrhizal association to protect host plants against toxic conditions

Although most studies concerning nutrition in the ericoid mycorrhizal association have concentrated on nitrogen and phosphorus, several have also dealt with the enhanced uptake of other essential and non-essential elements. *Hymenoscyphus ericae* has the ability to regulate the uptake of iron into host plants (Shaw & Read 1989). This fungus has a high affinity for iron even at very low external concentrations. This trait is expressed by the fungus in culture and in association with a host (Smith & Read 1997). Regulation of iron uptake may be due to the release of Fe-specific siderophores (Schuler & Haselwandter 1988).

Hymenoscyphus ericae also has a strong affinity for a number of other metals (Bradley *et al.* 1981, 1982; Denny & Ridge 1995). The effect of pH on growth and copper and zinc uptake in ericoid mycorrhizal fungi was assessed during incubation in liquid nutrient medium containing either 0.25 mM copper or 2.0 mM zinc and adjusted to pH 2, 3, 4, 5 or 6 (Gibson & Mitchell 2005a). After incubation, dry mass and mycelial metal content were determined and growth was expressed as a tolerance index, *i.e.* dry mass in the presence of metal as a percentage of dry mass in the absence of metal. Initial medium pH had a significant effect on both tolerance index and metal accumulation. Tolerance indices were highest at pH 2, with several isolates showing a stimulation of growth (*i.e.* tolerance

index > 100 %) at this pH. Tolerance index decreased at higher initial pH values and this reduction coincided with an increase of copper and zinc in the mycelium.

The copper and zinc concentrations resulting in 50 % reduction in mycelial dry mass of ericoid mycorrhizal fungi fall in the range of 0.3–0.9 mM copper and 1.2–5.5 mM zinc (Bradley *et al.* 1982; Burt 1984; Gibson & Mitchell, in press). Isolates from metal-polluted sites were not necessarily more tolerant than isolates from unpolluted sites. The apparently inherent, low metal-sensitivity of ericoid mycorrhizal fungi may be due to selection under natural conditions (Burt *et al.* 1986), since isolates are typically found in acidic heathland soils, which contain high levels of iron, aluminium and manganese (Marschner 1995). Resistance to these metals may confer resistance to other metals such as copper or zinc, which are not normally found in excessive levels in heathland soils.

Investigations have also determined the protein profile and gene expression of a zinc tolerant strain of *O. maius* (Vallino *et al.* 2005). Under a high zinc concentration, the expression of 16 genes was altered by being either up- (9) or down- (7) regulated (Vallino *et al.* 2005). In two of the up-regulated genes, genes for an oxidoreductase and a hypothetical protein, the signal in the control was too low to enable the determination of expression level in the zinc-grown mycelium.

Ericoid mycorrhizal fungi can grow in the presence of mine spoil and differences in sensitivity are, again, not necessarily related to their origin (Gibson & Mitchell, in press). Mycorrhizal protection of a host is associated with a reduction in metal concentration within host shoots. The reduction in shoot copper accumulation may be due to sequestration of metals within the mycorrhizal root system (Bradley *et al.* 1982), or due to an exclusion mechanism operating at the mycorrhizal root surface (Gibson & Mitchell, in press). The type of mechanism involved may be dependent on either the isolate of ericoid mycorrhizal fungus or plant cultivar present in the association. An exclusion mechanism operating at the mycorrhizal root surface would mean that the fungus is protected as well as the plant. The production of mucilaginous slime around hyphae may act as an exclusion mechanism by restricting the movement of metal ions (Denny & Ridge 1995). The binding of metals within the mycorrhizal root system has been confirmed by ultra-structural studies (Dudderidge & Read 1982), where pectin-like substances have been observed in the interfacial matrix separating plant and fungal plasma-membranes within the colonized cells. Accumulation of metals also occurs in fungal vacuoles.

Most studies have described the protection against positively charged metals. However, many soils are contaminated with organic arsenic compounds as a result of applications of now banned pesticides (Meharg & Hartley-Whitaker 2002). The *C. vulgaris*/*H. ericae* association has been shown to survive on arsenate sites (Sharples *et al.* 2000a) and the protection is provided by arsenate-resistant fungi (Sharples *et al.* 2000b). Since arsenate is an analogue of phosphate, it is transported across the plasma-membrane via the phosphate co-transporter system (Meharg & Macnair 1992). Although arsenate–resistant ericoid mycorrhizal fungi accumulate arsenate, they have the capacity to reduce arsenate to arsenite, which is expelled from their mycelium without any interference with phosphate transfer (Sharples *et al.* 2000a,b, 2001).

7. Conclusions

Considerable advances have been made in the understanding of interactions between ericoid mycorrhizal fungi and their plant partners. There is growing evidence that the fungi involved in these associations are more diverse than was previously thought (Cairney & Meharg 2003). The major events involving the attachment, penetration and internal proliferation of the fungus in the outer cells of the root have been established (Dudderidge & Read 1982). These associations have been shown to be well adapted to the heathland environment and they can also tolerate mine wastes. The ability of these associations to adapt to such a broad range of habitats is probably due to the plastic nature of each partner (Cairney & Meharg 2003). However, the reasons for the differences in adaptation against low nutrient conditions and mycorrhizal amelioration of mine spoil toxicity with different ericoid mycorrhizal fungi and plant partners are not completely understood.

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The BMS Roadshow will be on display at the RHS Chelsea Flower Show, 23–27 May, 2006

During 2005 the BMS Roadshow was awarded Silver-Gilt or Gold Medals at every Royal Horticultural Society show it attended. Our displays fall within the range of the RHS Lindley Medals – awarded for ''…excellence of exhibits of special scientific or educational interest''. The Roadshow's RHS Medal award record since it was established is Tatton Park 2004, **Silver-Gilt**; Malvern Autumn 2004, **Gold**; Malvern Spring 2005, **Silver Gilt**; Tatton Park 2005, **Gold**; Malvern Autumn 2005, **Gold**.

Council decided, at its September meeting, to enter the BMS Roadshow for the 2006 Chelsea Flower Show with the intention of basing the entry largely on the existing Roadshow materials which have proved so popular with both the public and RHS judges. We now know that we have been offered an exhibition site by the RHS, as one of the Lifelong Learning Displays in the Great Pavilion – site number GPA/2.

Why don't you come along to Chelsea and see your Roadshow?

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