



The Structure and Function of the Ericoid Mycorrhizal Root

D. J. READ

Department of Animal & Plant Sciences, University of Sheffield, PO Box 601, Sheffield, S10 2UQ, UK

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The uniformity of structure of the anatomically simple ericoid mycorrhizal hair root across many plant families, including Epacridaceae, that are diagnostic of heathland, and the characteristic restriction of its occurrence to nutrient impoverished soils, are both emphasized. The extent to which the predominantly ascomycetous fungal endophytes of these roots are taxonomically related is discussed. In functional terms, the role of the mycorrhiza in nutrient mobilization is evaluated on the basis of experiments with ericaceous plants. The considerable saprotrophic potential of endophytes such as *Hymenoscyphus ericae* is demonstrated and the significance of this for nitrogen (N) and phosphorus (P) nutrition of plants growing in sclerophyllous litter of high C:N and C:P ratios is discussed. The need to carry out experiments using epacrid hosts is stressed. It is considered that the selective provision, by ericoid mycorrhizal fungi, of access to recalcitrant organic sources of N and P facilitates niche differentiation and so contributes to the maintenance of species diversity which is a feature of heaths with a significant component of epacrid or ericaceous plants particularly in the southern hemisphere. © 1996 Annals of Botany Company

Key words: Ericoid mycorrhiza, hair root, heathland, nitrogen mobilization, Epacridaceae.

INTRODUCTION

In 1979 Specht described the heathlands of the world as being united by their evergreen sclerophyllous nature, by the presence, but not necessarily the dominance of the families Diapensiaceae, Empetraceae, Epacridaceae, Ericaceae, Grubbiaceae, Prionotaceae and Vacciniaceae, and by their ecological restriction to soils very low in plant nutrients.

It has subsequently been argued (Read, 1983; Read and Kerley, 1995) that emphasis upon phenology of above-ground parts has diverted attention from a below-ground structure, the ericoid mycorrhizal root, which has even greater uniformity through the families listed by Specht, than any aspect of the shoots. This structure, long known to be a characteristic feature of ericaceous genera of the northern hemisphere (Rayner, 1915, 1925, 1929), was first described in the Epacridaceae by McLennan (1935). It is characterized by reduction of its vascular and cortical tissues, by the absence of root hairs, and by the presence in what would be the piliferous zone of a conventional plant root, of swollen epidermal cells occupied by mycorrhizal fungi (Fig. 1). Ericoid mycorrhizal roots have now been observed in a large number of epacrid genera (Table 1). The individual roots, as a result of their anatomical simplification, are delicate structures, often referred to as 'hair-roots' usually each having a diameter in the distal regions of less than 100 μm (Fig. 2A, B). Collectively, the hair-roots form a dense fibrous root system the bulk of which is concentrated towards the surface of the soil profile (Dodd *et al.*, 1984; Pate, 1994).

While the soils in which plants with ericoid mycorrhizal roots flourish are rightly characterized by their impoverished nutrient status, they cover such a broad latitudinal range

that they show a great diversity of hydrological conditions. Thus in the southern hemisphere epacrids are found on the permanently moist soils of the Magellanic tundra complex of Patagonia (Pisano, 1983) and the *Sphagnum* mires of New Zealand (Wardle, 1991) as well as on the dry sand-plains of Australia. Each of these very different moisture regimes causes a distinctive pattern of seasonal development of the essentially ephemeral ericoid root system, it being active in the moist winter season in the sand-plain heath environment (Read, 1983; Bell, Pate and Dixon, 1994) but in the drier summer season in peat dominated systems of high latitudes.

It is important to bear this diversity of habitat type in mind when considering functions of the ericoid root. While there is an apparent logic and appeal in the assumption that a structure as uniform as this should also be uniform in its function, it will be shown below that such structures have a wide range of functional attributes. At the very least it would be wise to determine which, if any, of these attributes are important in a given ecological circumstance, and to bear in mind that the ericoid mycorrhizal root is part of an overall adjustment of epacridaceous or ericaceous species to the extreme nutritional impoverishment of heathland soils. Only by evaluating the above and below ground attributes of these plants in an integrated manner will we eventually achieve a realistic understanding of what provides 'fitness' in their peculiarly harsh environments.

The fungi forming ericoid mycorrhiza

It has now been firmly established that fungi isolated from epidermal cells of hair roots of the Ericaceae (Fig. 3) typically produce dark coloured slow growing sterile and dematiaceous mycelia in agar cultures. Many such isolates

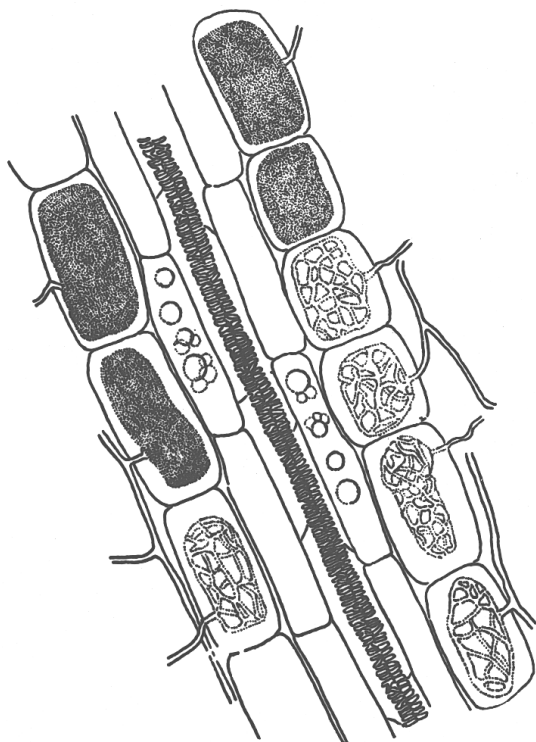


FIG. 1. The ericoid mycorrhizal root of *Epacris impressa* as originally depicted by McLennan (1935). Epidermal cells heavily colonized by hyphal complexes are seen to enclose narrow cells of the exodermis, endodermis and the monarch stele.

form zig-zag chains of arthroconidia in culture (Burgeff, 1961; Pearson and Read, 1973) a feature which has led Dalpé, Litten and Sigler (1989) to assign them to the genus *Scytalidium* (Fig. 4). Some of these isolates also produce apothecia which has enabled them to be identified as the ascomycete *Hymenoscyphus ericae* (Read) Korf and Kernan (Read, 1974). Comparative analysis of ribosomal DNA sequences of an isolate of *Vaccinium* identified as being *Scytalidium vaccinii* and of *H. ericae* suggest that there is an anamorph-teleomorph relationship between these two fungi (Egger and Sigler, 1993).

Until recently the question of the identity of fungi forming ericoid mycorrhiza in Epacridaceae had not been addressed. Two studies, one carried out in eastern (Reed, 1987) the other in western Australia (Hutton, Dixon and Sivasithamparam, 1994) have now added considerably to our knowledge. They indicate that isolates obtained from epidermal hyphal complexes (Fig. 5) have broadly similar culture characteristics to those seen in their ericaceous counterparts of the northern hemisphere. Again, they are dark coloured slow growing sterile dematiaceous fungi. It is apparent on the basis of light (Reed, 1989; Hutton *et al.*, 1994) and electron (Allen *et al.*, 1989) microscope studies revealing the presence of simple septa that they are of ascomycetous rather than basidiomycetous affinity. These observations coupled with that of Reed (1989), subsequently confirmed by Read and Reed (unpubl. res.), that fungal isolates of Epacridaceae readily form typical root ericoid

TABLE 1. Records of epacrid genera that have been reported to have ericoid mycorrhiza

Epacrid genus	Reference
<i>Acrotiche</i>	Reed, 1987
<i>Andersonia</i>	Reed, 1987; Hutton <i>et al.</i> , 1994
<i>Astroloma</i>	Hutton <i>et al.</i> , 1994; Bell <i>et al.</i> , 1994
<i>Brachyloma</i>	Reed, 1987; Hutton <i>et al.</i> , 1994
<i>Conostephium</i>	Reed, 1987; Hutton <i>et al.</i> , 1994
<i>Cyathodes</i>	McNabb, 1961
<i>Dracophyllum</i>	McNabb, 1961; Allen <i>et al.</i> , 1989; Logan <i>et al.</i> , 1989
<i>Epacris</i>	McLennan, 1935; Reed, 1987
<i>Leucopogon</i>	McNabb, 1961; McGee, 1986; Reed, 1987, 1989; Brundrett and Abbott, 1991; Logan <i>et al.</i> , 1989; Hutton <i>et al.</i> 1994; Bell <i>et al.</i> , 1994
<i>Lissanthe</i>	Reed, 1987
<i>Lysinema</i>	Reed, 1987; Hutton <i>et al.</i> , 1994
<i>Melichrus</i>	Reed, 1987
<i>Monotoca</i>	Reed, 1987
<i>Needhamiella</i>	Reed, 1987
<i>Oligarrhena</i>	Reed, 1987
<i>Pentachondra</i>	McNabb, 1961; Reed, 1987
<i>Richea</i>	Reed, 1987
<i>Rupicola</i>	Reed, 1987
<i>Sphenotoma</i>	Reed, 1987; Hutton <i>et al.</i> , 1994
<i>Sprengelia</i>	Reed, 1987
<i>Styphelia</i>	Reed, 1987
<i>Trochocarpa</i>	Reed, 1987
<i>Woollisia</i>	Reed, 1987

mycorrhiza in hair roots of Ericaceae, and *vice versa*, are strongly suggestive of close relationships between the fungi. However, on the basis of pectic zymogram analysis it was reported (Hutton *et al.*, 1994) that none of the isolates obtained from 14 genera of Western Australian epacrids produced banding patterns which perfectly match those of ericaceous isolates. Notwithstanding this, the similarities between published zymograms of some of the isolates, notably Ec2 and Ec3 obtained from *Andersonia* and those of ericaceous isolates 100 and 101 are striking. The appearance of these two epacrid isolates in culture is also very reminiscent of *H. ericae*.

There is a need for DNA sequence analysis of these isolates to be run in parallel with studies of their functional attributes or when grown with epacrid or ericaceous hosts. The work of Perotto *et al.* (1995) is moving in this direction.

Some workers have reported the isolation of *Oidiodendron* spp. from mycorrhizal hair roots of ericaceous species (Burgeff, 1961; Couture, Fortin and Dalpé, 1983; Dalpé, 1986, 1991; Douglas, Heslin and Read, 1989; Xiao and Berch, 1992). To date there appear to be no reports of these fungi being isolated from epacrid roots. The banding patterns produced in pectic zymograms by a series of European and North American isolates of *Oidiodendron* were shown by Hutton *et al.* (1994) to be distinct from those of fungi obtained from epacrid mycorrhiza.

In addition to these records of fungi isolated from typical ericoid mycorrhiza, there are a few reports in the literature of colonization of epacrid and ericaceous roots by arbuscular

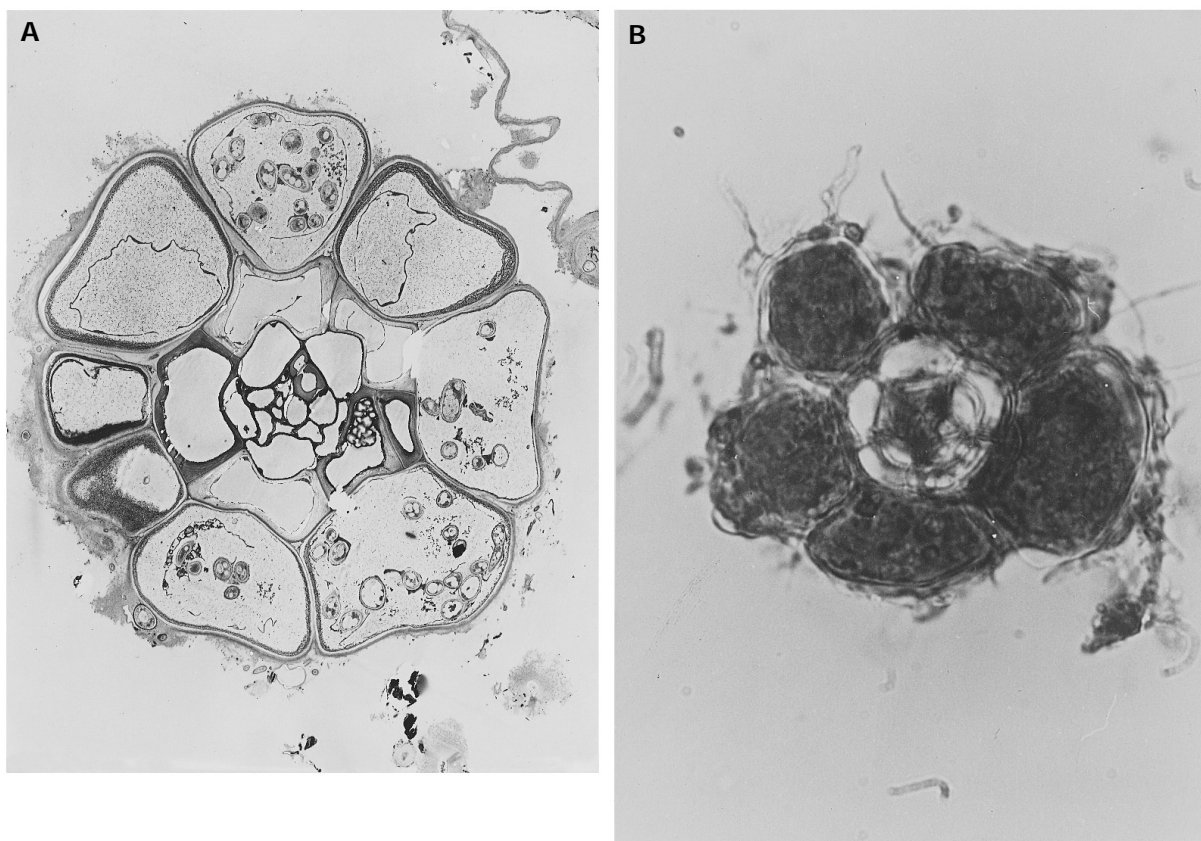


FIG. 2. A, Transverse section of ericoid hair root of *Leucopogon ericoides* Smith R. Br. fixed in glutaraldehyde and embedded in Spurr's resin. Root diameter approx. 67 μm . Material fixed sectioned for TEM and photographed by Suzanne Bullock. This section is taken in a mature region of the hair root and shows relatively light colonization. B, Transverse hand section of young hair root of *Calluna vulgaris* indicating very heavy colonization of all of the epidermal cells by a mycorrhizal endophyte. Root diameter approx. 70 μm .

(VA) and ectomycorrhizal (ECM) fungi. Bellgard (1991), without mention of ericoid colonization, reports the presence of VA associations in *Brachyloma*, *Epacris* and *Leucopogon* growing on Hawkesbury sandstone, while McGee (1986) observed ericoid colonization in the latter genus but VA and ectomycorrhiza in *Astroloma*. Similarly in Ericaceae, plants which would normally have ericoid infection have been reported to be colonized by ectomycorrhizal (Largent, Sugihara and Wishner, 1980; Dighton and Coleman, 1991) and VA (Johnson, Joiner and Crews, 1980; Koske, Gemma and Englander, 1990; Dighton and Coleman, 1991) fungi. Since in none of these reports were attempts made to determine the functional status of the fungal colonization, their status remains uncertain. There is increasingly evidence that when growing from a true 'host' mycorrhizal fungi of the VA type have sufficient inoculum potential to enable penetration of nearby plants which are not normally colonized (Francis and Read, 1995). The outcome of such colonization can, however, be detrimental to the 'non-host' and under these circumstances any suggestion that the occurrence represents a mycorrhizal symbiosis should be treated with caution.

Leake and Read (1991) have stressed the need to satisfy the requirements of Koch's (1912) postulates when assessing the status of any putative mycorrhizal association. This requires not only that a healthy structural relationship

between host and fungal inoculant is produced under conditions which are free of exogenous sources of simple sugars, but also that some measures of host response be obtained. By growing seedlings of *Calluna vulgaris* under defined conditions in the presence of a range of fungal isolates of ericoid roots, they showed that while some including *H. ericae*, *S. vaccinii* and to a lesser extent *O. griseum* gave a positive growth response in the seedlings, others were inhibitory. Ideally these studies should be carried out in natural soil but the complication associated with the need to sterilize such substrates makes this problematical.

It is arguable also that to challenge the delicate hair roots of an epacridaceous or ericaceous seedling with vigorous inoculum of a single fungus is unrealistic, since in nature the emerging radical immediately enters a complex community of microorganisms. The use of mixed inocula of putative endophytes and saprotrophes would enable determination, either by use of *in situ* immunocytochemical identification, or by sequence analysis following subsequent re-isolation, of which fungi gained access to and formed compatible associations with a particular host species. Such studies if carried out in a range of hosts and substrates would help to provide answers to the challenging question of the relative importance of host and ecological specificity in determining the outcome of host-fungus interactions.



FIG. 3. Individual epidermal cell of *Calluna* released from the root axis by maceration after serial washing in distilled water, showing emergence of mycorrhizal fungus from hyphal complex occupying the cell. Such direct observation of fungal growth from the cell is desirable if prerequisite for any claim of mycorrhizal status.

What we know about functional aspects of the ericoid mycorrhiza

It arises from the essentially superficial pattern of distribution of ericoid mycorrhizal roots in the soil profile that they are in intimate contact with the detrital material produced as the above and below ground parts turnover. In an environment characterized by extremes of nutrient impoverishment it is clearly important to determine the extent to which these roots are directly involved in turnover processes.

The conventional view of the function of a root as a nutrient absorbing organ is that it provides effective interception of minerals released from organic polymers or insoluble salts by the activities of a decomposer population. Within this scenario mycorrhizal colonization has been interpreted simply as providing greater effectiveness in such mineral scavenging activities. There is, indeed, evidence that *H. ericae* can assimilate nitrate, ammonium (Bajwa and Read, 1986) (Fig. 6A) and phosphate (Pearson and Read, 1975) ions, and the importance of this should not be overlooked, in particular in sandy heathland soils of warmer regions. Significant amounts of nitrification can, for example, occur in these soils (Hannon, 1956) and in view of

the very low nitrate reducing ability of ericaceous (Havill, Lee and Stewart, 1974) and epacridaceous (Stewart, Pate and Unkovich, 1993) plants themselves, access to the nitrate ion may be largely dependent upon mycorrhizal colonization. Experiments have shown, however, that the fungi forming ericoid mycorrhiza also have saprotrophic capabilities sufficient to enable competition with decomposers, and so have exposed the possibility of direct involvement of the mycorrhizal root in mobilization of N and P from the organic residues which are the major repository of both of these elements in most heathland ecosystems (Read, 1983; Read and Kerley, 1995).

The first indication of this type of activity came from a study in which ^{15}N labelled ammonium was fed to mycorrhizal (M) and non-mycorrhizal plants of *Vaccinium* growing in sterile heathland soil (Stribley and Read, 1974). It was observed that despite having significantly greater yields and total nitrogen contents the M plants had lower ^{15}N enrichment, indicating that dilution of label by alternative N sources had occurred. In the absence of nitrification, organic residues were the only realistic candidates. This observation led to a series of analyses in which the saprotrophic potential of ericoid endophytes was examined in pure culture and in association with their host plants. In addition to an ability readily to use ammonium or nitrate as sole source of N *H. ericae* used amino-acids, (Bajwa and Read, 1986) (Fig. 6B, C) peptides (Bajwa and Read, 1985) of a range of chain lengths, and protein, the polymeric forms of organic N being broken down by the activities of an acid carboxy-proteinase enzyme (Leake and Read, 1989a, 1990a). When these experiments were repeated using plants grown in the M or NM condition, it was shown that substantial quantities of N assimilated from organic sources by ericoid fungi were transferred to the autotroph (Stribley and Read, 1980; Bajwa and Read, 1985, 1986; Bajwa, Abuarghub and Read, 1985).

The thrust of work in recent times has been towards evaluating the extent to which the saprotrophic capabilities revealed in studies using model N compounds, might be expressed also in natural environments where the element is likely to be contained in more complex polymers or to be precipitated with polyphenolic compounds.

Of the naturally occurring polymers which are a significant repository of N, chitin, particularly in soil horizons heavily exploited by mycorrhizal fungi, is likely to be amongst the most important. It is known to be a major constituent of the hyphal walls of *H. ericae* itself (Bonfante-Fasolo and Gianinazzi-Pearson, 1982). Leake and Read (1990b) showed that chitin, when supplied as sole N source to *H. ericae* in pure culture was able to support growth of the fungus. More recently Kerley and Read (1995) have grown *H. ericae*, which is likely itself to be the main potential source of fungal N in heathlands dominated by ericaceous plants, under aseptic conditions, and used its dead mycelium as a sole source of N for *Vaccinium* plants grown with and without mycorrhizal colonization. Mycorrhizal plants gained sufficient access to N contained in this substrate to enable significant increases of yield and N concentration (Figs 7, 8). Purified hyphal wall fractions can also provide N sources for *H. ericae* the culture filtrates of which after

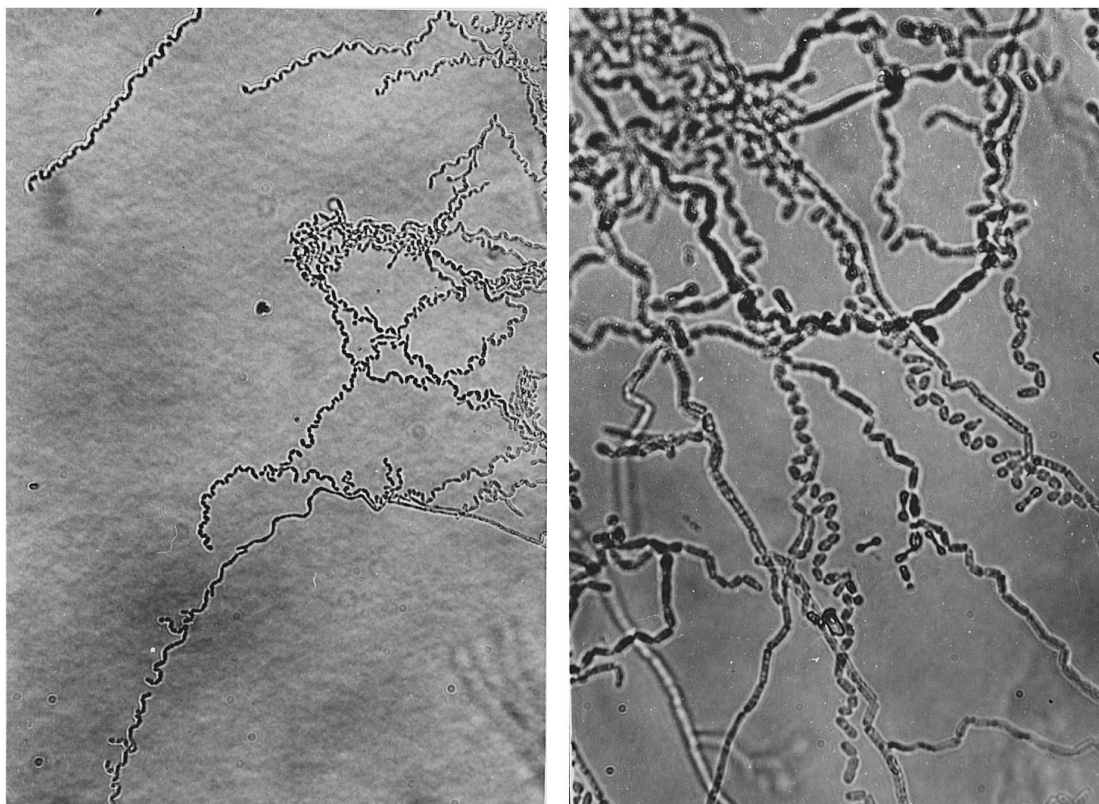


FIG. 4. Segmentation of hyphae of an isolate of *H. ericae* to zig-zag chains of arthroconidia which are characteristic of *Scytalidium*.

growth on such substrates reveal evidence of chitinolytic activity in the form of glucosamine residues (Kerley and Read, 1995).

Soluble protein released from plant and fungal tissues on senescence would also be accessible to fungi with well developed proteolytic potential, but the half-life of protein as a free component in mor-humus litters of the kind produced under polyphenol-rich heathland plants is likely to be short. Experiments using aqueous extracts of these materials, or tannic acid as a model polyphenolic compound, over a pH range characteristic of the soil produced from them, demonstrate the effectiveness with which protein is co-precipitated by tannins. Bearing in mind the very high concentrations of polyphenols typically found in sclerophyllous tissues of the ericaceous type (Jalal, Read and Haslam, 1982), it is probable that such precipitation will occur during breakdown of cellular compartmentation as senescence proceeds so largely removing free protein from circulation. Under these circumstances the key question would concern the extent to which the ericoid endophytes have access to protein-N that is precipitated in this way. Answers to these questions are beginning to emerge for ericaceous hosts but remain to be sought in the case of epacridaceous mycorrhiza.

It has been shown (Leake and Read, 1989*b*; Bending and Read, unpubl. res.) that *H. ericae* has considerable potential to mobilize protein N even when the source polymer is co-precipitated with polyphenols such as tannic acid. Its biomass yield is unrestricted (Fig. 9) and N is acquired from

such sources in amounts greater than those obtained when $\text{NH}_4\text{-N}$ is supplied at the same concentration (Fig. 10). This N can eventually be transferred to the host in sufficient quantity to enhance its growth and its release appears to be achieved by a combination of polyphenol-oxidase (PPO) and proteinase activities (Bending and Read, unpubl. res.). Assays of the latter (Fig. 11) suggest inhibition of the enzyme in the presence of tannic acid (Fig. 12) but part of this may be attributable to co-precipitation of protein and product in the presence of the phenolic compound.

The ability to degrade polyphenols, perhaps combined with ligninolytic activity (Haselwandter, Bobleter and Read, 1990) enables the fungus to achieve a broadly based attack upon the sclerophyllous residues which protect the scarce nutrient resources in heathland soils. While nitrogen may be quantitatively the most important of these, others notably phosphorus (P) may also be released by activities of this kind. *H. ericae* has been shown to release P from ferric and aluminum phytates which are thought to be the major sources of the element in acid organic soils (Mitchell and Read, 1986).

There have as yet been relatively few studies of the functional aspects of ericoid mycorrhiza in epacrids and these are clearly much needed. However, a recent examination of the responses of seedlings of four epacrid species (*Andersonia gracilis*, *Astroloma xerophyllum*, *Leucopogon conostephiodes*, and *Leucopogon kingianus*, now *Croninia kingianus*) (Bell *et al.*, 1994) lends general support to the view established from studies, reported above, of their

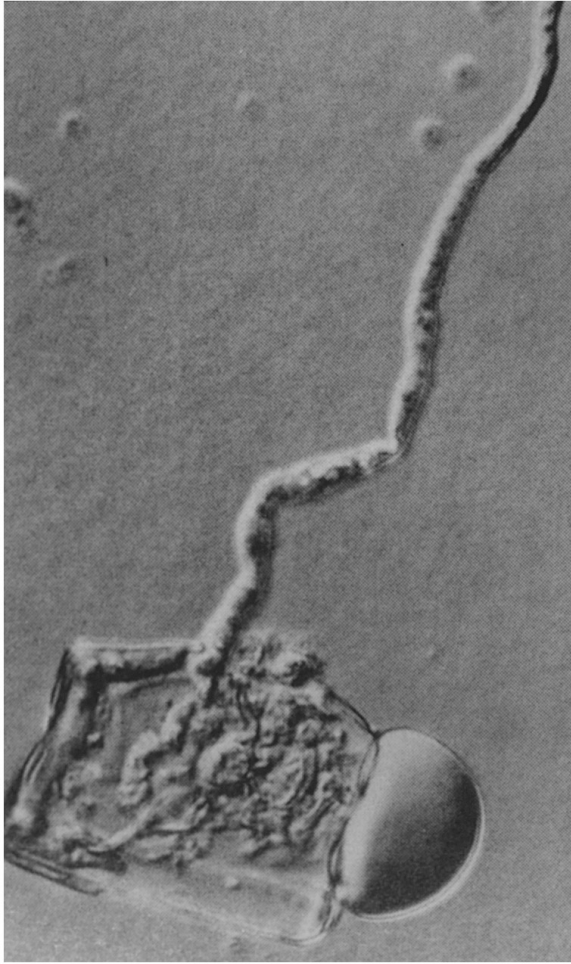


Fig. 5. Endophyte emerging from epidermal cell of *Leucopogon juniperinus* after serial washing of the hair root and plating on water agar (from Reed, 1987).

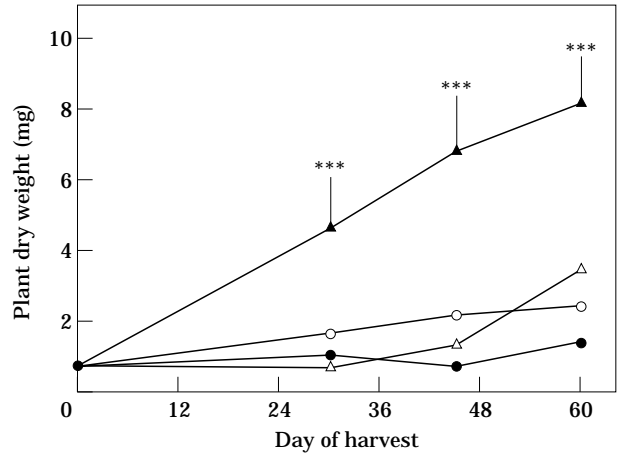


Fig. 7. Yield of *V. macrocarpon* grown in the mycorrhizal (M) and non-mycorrhizal (NM) condition with dead intact mycelium of *H. ericae* (IHE) as sole N source. Vertical bars represent l.s.d. $P = < 0.05$. *** Indicates significant difference between M + IHE and NM + IHE at $P < 0.001$ according to one way ANOVA. (From Read and Kerley, 1995.)

ericaceous counterparts, that the symbiosis plays a primary role in the acquisition of nitrogen for the plant. Seedlings of these species were transferred in minimally disturbed soil cores from the field to pot cultures in a glasshouse where they were supplied with distilled water, with complete nutrient solutions or with solutions containing only nitrogen or only phosphorus.

Three of the species showed significant positive responses of shoot height and plant dry weight to N added as NH_4NO_3 whereas addition of P as PO_4 led to little or no such growth response. Addition of complete nutrient solution resulted in dry matter yields not significantly greater than those observed in the N only treatment, a

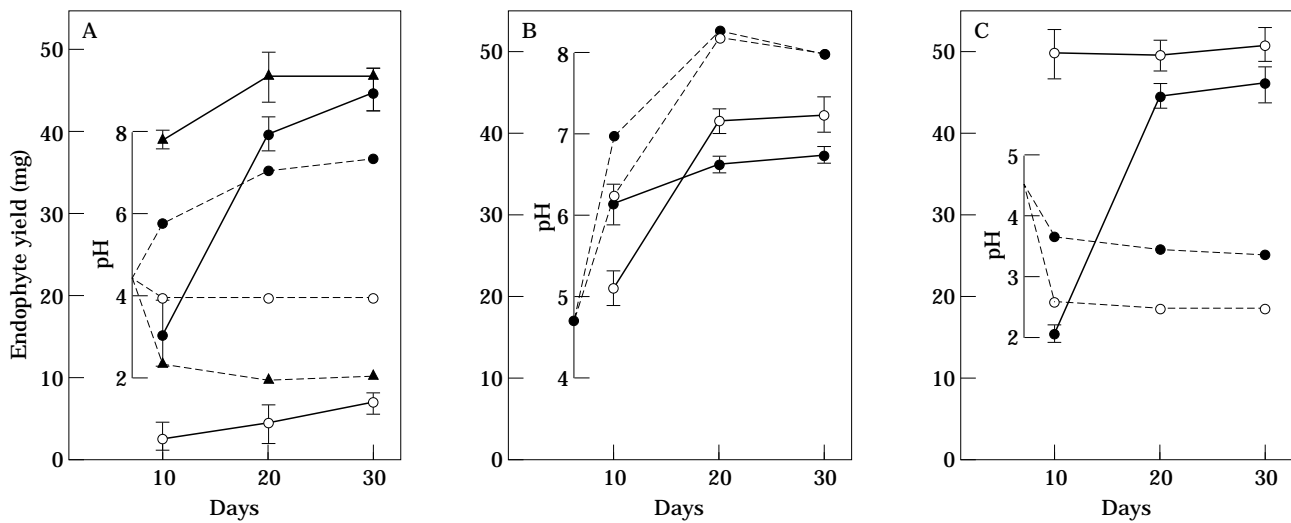


Fig. 6. Dry weight yields (—) of *H. ericae* and changes of pH (---) of media after growth of the fungus on nitrate, ammonium or a series of acidic and basic amino-acids as sole sources of N. (A) Mineral (\blacktriangle , NH_4 ; \bullet , NO_3) or minus N (\circ , control) treatments, (B) acidic amino acids (\bullet , Aspartic acid; \circ , Glutamic acid) and (C) basic amino acids (\bullet , 2 Amino-butyric; \circ , Arginine). (From Bajwa and Read, 1986.)

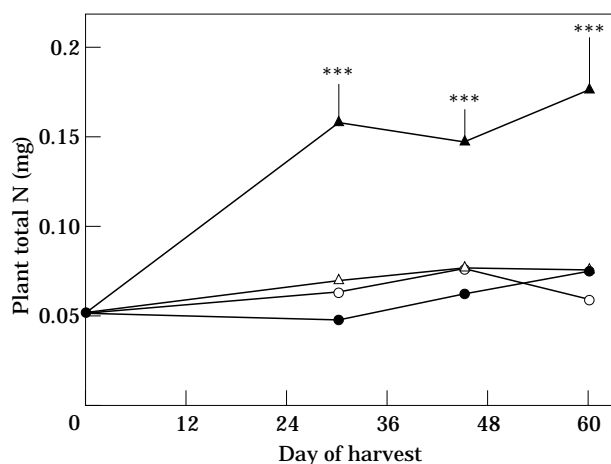


FIG. 8. Whole plant nitrogen content (mg plant dry weight) of *V. macrocarpon* grown and analysed as described in Fig. 7. (From Read and Kerley, 1995.)

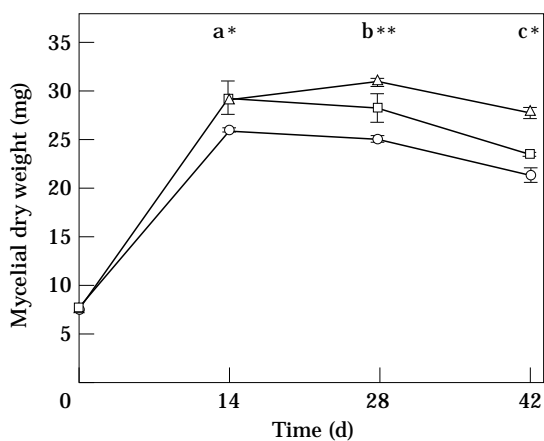


FIG. 9. Dry weight yield of mycelium of *H. ericae* grown with pure protein (□), protein precipitated with tannic acid (△), or with basal medium containing ammonium (○) (control) N, as sole N sources. Letters indicate significance of differences between treatments at a given harvest as determined by one-way ANOVA. a, Treatments significantly different except pure protein *vs.* precipitated protein. b, Significant difference between control and precipitated protein. c, All treatments significantly different. ** Indicates differences significant at $P < 0.01$. * Indicates differences significant at $P < 0.05$. (From Bending and Read, unpubl. res.)

further feature suggestive of a pivotal role of this element in determining plant responses. *L. kingeanus* failed to respond to any of the treatments. Labelling of the complete or N treatments with $^{15}\text{NH}_4$ or $^{15}\text{NO}_3$ showed that both forms of N were taken up and incorporated into plant insoluble N. While apparently confirming the importance of nitrogen acquisition for epacridaceous plants these experiments do not inform us as to the role of the mycorrhiza in qualitative or quantitative aspects of N assimilation and leave unanswered the important question of the extent to which colonization provides the plant with access to organic residues in the field.

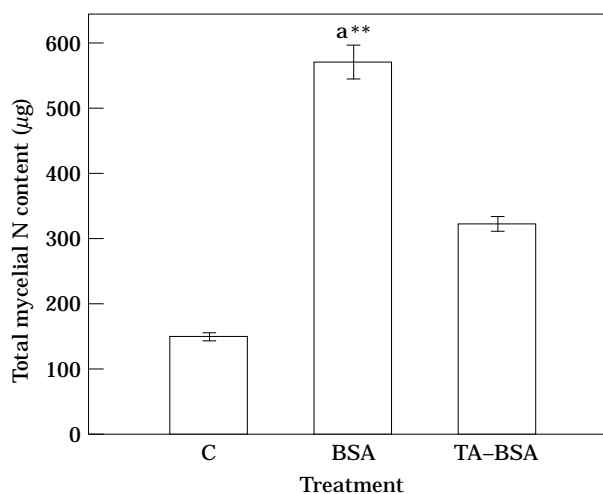


FIG. 10. Total nitrogen content of harvested mycelium of *H. ericae* at final harvest after growth with pure protein (BSA), protein precipitated with tannic acid (TA-BSA), or on basal medium with ammonium as N source (C). a**, Indicates all treatments significantly different at $P < 0.01$ according to one-way ANOVA. (From Bending and Read, unpubl. res.)

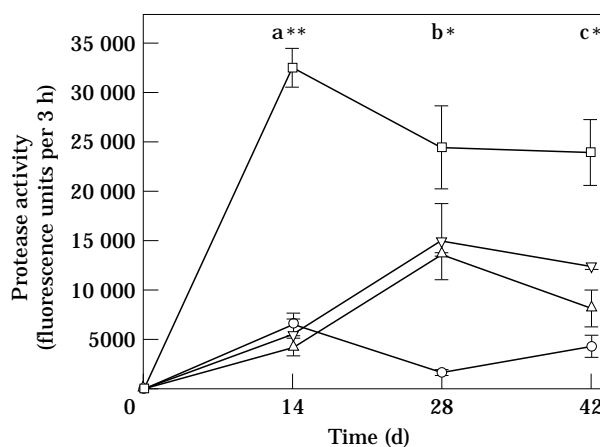


FIG. 11. Extracellular protease activity of *H. ericae* measured over a time-course in media containing pure protein (□), pure protein precipitated with tannic acid (▽), the culture filtrate of protein-tannic acid treatment (△), and the basal medium without protein (○). a**, Indicates activity in protein treatment significantly different from protein-tannic acid and control at $P < 0.01$. b*, Indicates both protein and protein tannic acid treatments significantly different from control at $P < 0.05$. c*, Indicates all treatments significantly different except protein-tannic acid and culture filtrate of protein-tannic acid at $P < 0.05$. (From Bending and Read, unpubl. res.)

DISCUSSION

Both in the managed *Calluna*-type heathlands of the northern hemisphere (Gimingham, 1972) and in the natural heaths of Australasia (Bell, Hopkins and Pate, 1984) fire is an important factor in the nutrient economy of the ecosystem. In both types of community burning has a particular impact upon the N economy of the system, up to 80% of the fund of nitrogen that has accumulated between burns being lost (Pate and Dell, 1984). Similar figures have been suggested in Europe (Allen, 1964). Chapman (1967) showed that volatilization of N during a burn in *Calluna*

COMPARTMENTATION OF NITROGEN ACQUISITION IN HEATHLAND ECOSYSTEMS

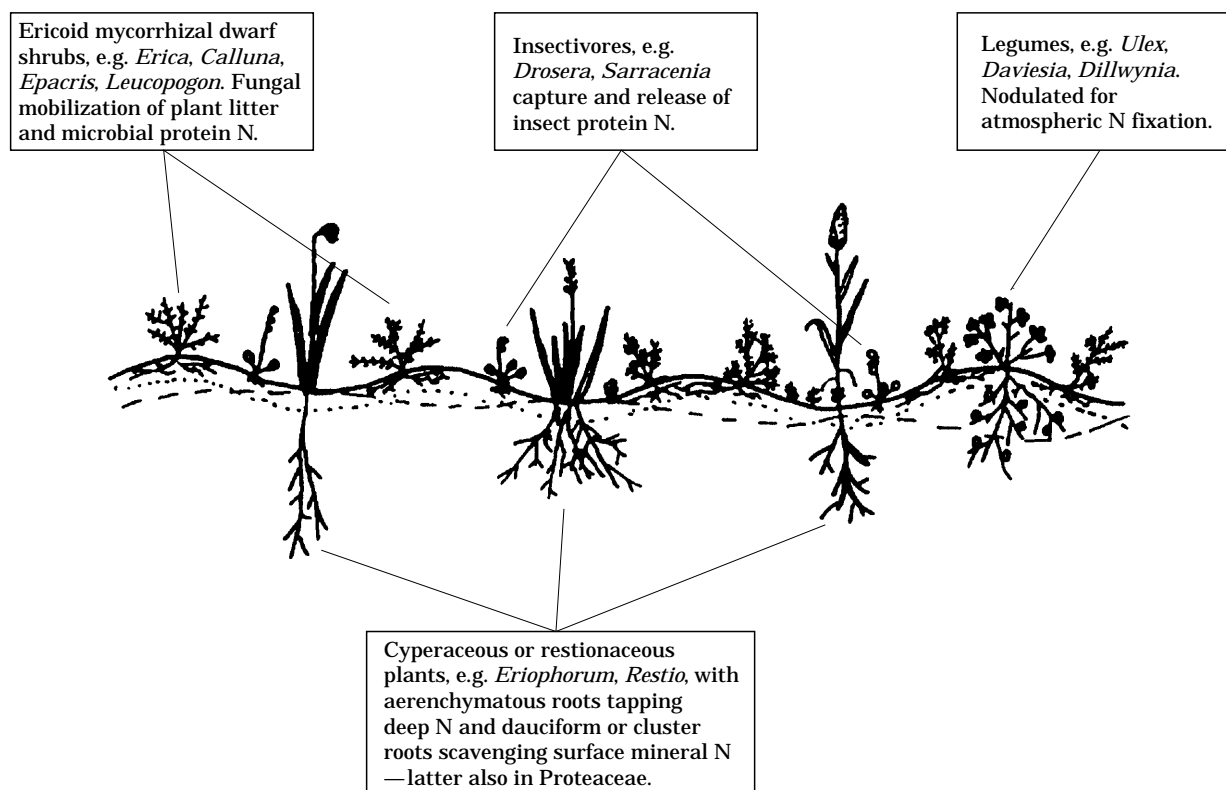


FIG. 12. Diagrammatic view of possible processes whereby niche separation in heathlands of northern and southern types might arise through mutualistic or structural modifications which provide access to qualitative different sources of the major element nitrogen.

heathland was equivalent to 173 kg ha^{-1} and that because cumulative inputs from rainfall in the 12 year period between fires was only 62 kg serious N deficits occurred. In Europe concerns over deficits in the N budget have been replaced in recent times by considerations of excess deposition, inputs of pollutant N in the form of NH_4 and NO_3 having reached in excess of 30 kg ha^{-1} in some heathlands (INDITE, 1994). Nitrogen saturation is now thought to be promoting the process whereby ericaceous plants are being progressively replaced in what were the heathlands of north-west Europe by grasslands (Heil and Diemont, 1983). In effect, N saturation removes the advantages of nutrient conservation associated with sclerophylly, as well as those derived from the ericoid mycorrhiza which, it is proposed, has evolved to provide selective access to the conserved resource. Instead it favours those species able rapidly to respond to surges of mineral N availability.

Epacrids still flourish in the relatively unpolluted heathlands of Australasia, and it is reasonable to hypothesize that they do so in some measure as a result of those attributes shown above to be features of ericoid mycorrhizas. There is clearly a need to explore further the functional relationships between the mycorrhiza of epacrid and ericaceous species. Amongst the attributes of particular interest in the naturally fire-prone epacrid habitat are the nature and distribution of fungal propagules in the post fire environment, the

relationship between seedling establishment and mycorrhizal colonization, and the role of the mycorrhiza in the processes of nutrient acquisition through the inter-fire cycle.

In an attempt to evaluate the possible contribution of mycorrhiza to the determination of the structure of wet heathland communities of the northern hemisphere Read (1993) presented a schematic view of the manner whereby distinctive mutualisms, together with modifications of root distribution and anatomy, might promote species diversity by enabling exploitation of different sources of the critical growth limiting element nitrogen. In this, the co-existence of ericaceous, leguminous and carnivorous species typically seen in heaths of moderate acidity, was facilitated by their abilities to use sources of N derived respectively, from soil organic matter, the atmosphere and captured animals. Structural modifications, in particular production of aerenchyma, enables cyperaceous species to penetrate water-logged horizons where they exploit N sources, including organic forms (Chapin, Morilanen and Keilland, 1993), untapped by the other groups that are essentially surface rooting.

The species diversity seen in heathlands containing epacrids is generally greater than that seen in those dominated by ericaceous species but it appears that there is a commensurate increase in the range of specialisms which they exhibit (Lamont, 1982, 1984; Pate, 1994). It can

therefore be hypothesized that the same niche separation occurs (Fig. 12). Amongst the distinctive families of southern heaths the Proteaceae and Restionaceae are characterized by the production of cluster roots. These structures are formed in the same superficial horizons of the soil profile as are ericoid roots, where they also exploit the region of actively decomposing litter (Lamont, 1984). Though spatial segregation appears not to occur there remains the possibility of functional differentiation between ericoid and cluster-root systems. As far as is known the main function of cluster roots is to enhance the capture of available phosphate ions (Malajczuk and Bowen, 1974), although they and their associated bacteria may also be involved in the mobilization of these ions. If this is the case while proteoid roots will scavenge for nutrients, including N, in mineral form, ericoid roots in the same substrate should have the potential to exploit organic nitrogen residues. Evidence to support functional segregation comes from the study of Stewart *et al.* (1993) who observed sufficient nitrate reducing ability (NRA) in shoots and roots of three proteaceous genera (*Banksia*, *Petrophile* and *Stirlingia*) to suggest that they would assimilate nitrate in nature. In contrast the two epacrid species *Astroloma macrocalyx* and *Conostephium pendulum* showed barely detectable NRA even after feeding of nitrate via the transpiration stream.

Other plant families with widespread representation in epacridaceous heaths but which are absent or of little importance in the northern hemisphere are Rutaceae, Dilleniaceae and Compositae, most members of which would be expected to be colonized by VA fungi. This type of mycorrhiza has been reported, for example, in *Boronia* (Rutaceae), *Hibbertia* (Dilleniaceae) and *Helichrysum* (Compositae) (Lamont, 1984). It appears that the less fibrous root system of plants such as these penetrate soil more deeply being of Types I and 4 (Dodd *et al.*, 1984) or Type R3 (Pate, 1994) a feature providing spatial separation from epacrids. In addition, while VA colonization will enhance their ability to scavenge for P, members of two of these genera *Helichrysum* and *Hibbertia* have been shown to develop significant NRA (Stewart *et al.*, 1993), again suggesting the likelihood of nutritional as well as spatial niche differentiation between these plants and those with ericoid mycorrhiza.

Recognition of these patterns leads to the suggestion that selection favouring a range of specialisms has been important in enabling the co-existence of taxonomically distinct species in Australian heathland systems, where the greatest diversity is found on the least fertile soils (Pate and Hopper, 1993). This situation contradicts Tilman's equilibrium model of plant competition (Tilman, 1982, 1988) which predicts that in resource poor environments diversity will be low because few species can survive such impoverishments. Rather, it suggests that over very long periods, evolutionary selection of distinctive mutualisms has facilitated co-existence of species in diverse assemblages. It is a measure of the success of the ericoid mycorrhizal mutualism within this range of specialisms that it is uniformly present across all the families which ecologists such as Specht (1979; Specht and Rundel, 1990) have recognized as being most characteristic of impoverished heathland ecosystems.

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