Mycorrhizas in ecosystems

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Summary. The results of analyses of the distribution, structure and function of ericoid, ecto and vesicular-arbuscular mycorrhizas are used to challenge the conventional view, which was based largely upon studies of isolated plants and excised plant roots under controlled conditions, that the symbiosis is primarily involved in the capture of phosphate ions. In nature, each mycorrhizal type is associated with an ecosystem and soil environment with distinctive characteristics in which selection has favoured the development of a particular range of attributes. These attributes are evaluated and their importance for the individual plant and for the ecosystems in which they occur is assessed. It is concluded that knowledge of the full range of functions of each mycorrhizal type is essential for an understanding of the distribution and dynamics of the ecosystem in which it predominates.

Key words. Ericoid mycorrhiza; ectomycorrhiza; VA mycorrhiza; ecosystem; nutrients; organic matter.

Introduction

In the century since mycorrhizas were first described much progress has been made towards an understanding of the structure and function of the symbiosis in individual roots and in single plants grown under laboratory conditions. The challenge now is to determine the extent to which the results obtained in such studies are of relevance to the real world in which plants and their fungal symbionts occurs as communities containing mixtures of interacting individuals and species, all exposed to fluctuating environmental conditions. These are the circumstances in which mycorrhizal associations evolved and in which ultimately their significance must be assessed. The differences between, and the diversities within, ecosystems combine to present the major obstacle to our understanding.

In the face of such diversity the application of generalizing principles has enabled us to recognize that specific suites of climatic and edaphic conditions have led to the selection of distinctive types of mycorrhiza each dominating in a defined biome[112]. Thus, species with ericoid mycorrhizas predominate on mor humus soils of high latitudes and altitudes, ectomycorrhizal species predominate in forest ecosystems with surface litter accumulation at intermediate altitudes and latitudes, and plants with vesicular arbuscular mycorrhizas dominate herbaceous and woody plant communities on mineral soils at lower latitudes (fig. 1).

It must be recognized, however, that the activities of man have profoundly changed this climatically and edaphically determined pattern of distribution, primarily through deforestation[36]. In the temperate lowlands there has been widespread replacement of largely ectomycorrhizal deciduous forests by pastoral and agricultural systems based upon herbaceous plants with VA mycorrhizas, while in the uplands of both temperate and boreal zones deforestation has often led to the replacement of ectomycorrhizal biomes by heathlands in which species with ericoid mycorrhizas are dominant.

While it is helpful in conceptual terms to recognize general patterns of distribution, the more critical question from the ecological point of view concerns the extent to which, and the mechanisms whereby, the characteristic mycorrhizal types influence the success of the individual plants, the plant species, and hence the ecosystem dynamics of the biomes themselves. To answer these questions a combination of laboratory and field approaches is required. This paper provides a summary of the present state of knowledge and highlights some important gaps in our understanding. It deals with the role of the different major types of mycorrhiza under stable circumstances, within their characteristic biomes, proceeding from ericoid through ecto to VA dominated systems.

The role of ericoid mycorrhizas in heathland ecosystems

Plants with ericoid mycorrhizas occur as more or less pure stands forming dwarf-shrub heaths covering fringe areas of the globe in which, for climatic reasons or as a result of deforestation, soil degeneration has occurred. We should recognize, however, that the restriction of ericaceous heaths today is a feature of the relatively warm mid-interglacial period and that during glacial times species with ericoid infection, notably members of the genera *Empetrum* and *Vaccinium* have dominated far more extensive tracts of the major continents. When growing as understorey species in the boreal forest and in Mediterranean types of vegetation, they are probably relicts of populations established under colder conditions which restricted tree growth[13,134]. In Mediterranean vegetation, as in other heathlands of the world today, the ericoid elements, either represented by ericaceous or epacridaceous species, are most strongly associated with strongly leached and nutrient poor soils[135] in which the major growth limiting nutrient is nitrogen[99].

Recalcitrance of organic matter is the characteristic feature of environments in which ericaceous plants become dominant often to the exclusion of all other higher plant species. They have even been referred to as 'humus

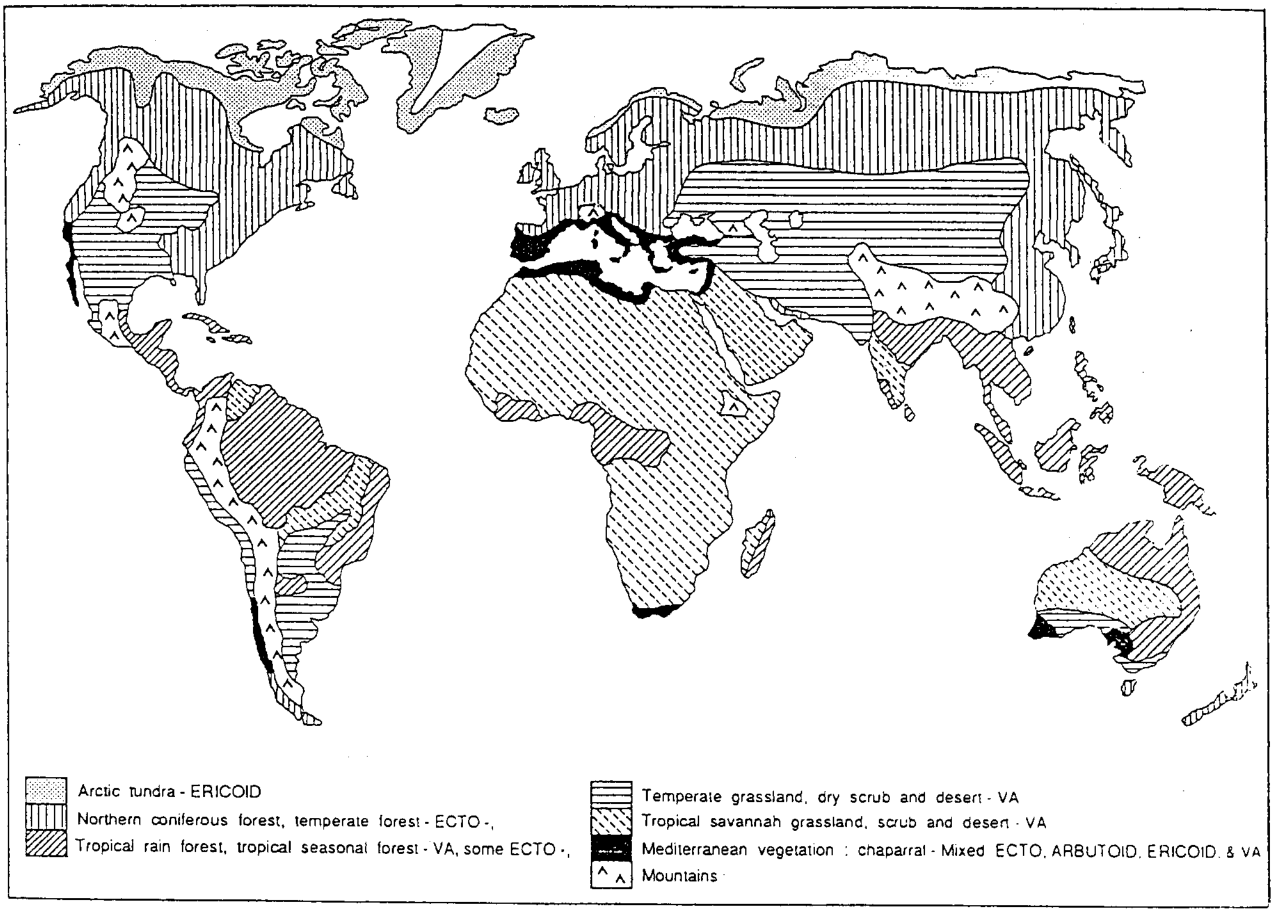

Figure 1. The distribution of the major terrestrial biomes of the world, demonstrating the close relationships between identifiable systems and particular mycorrhizal types.

plants'[36]. However, to consider this soil feature alone is to oversimplify the situation. Leaching, the loss of base cations, and associated reduction of pH all contribute to the production of a syndrome in which mineralization of nutrients is inhibited so that organic matter accumulates as raw humus, organic acids occur in solution in their most toxic undissociated form and metallic cations show maximum solubility (fig. 2). The final product is a heathland or tundra ecosystem in which a small number of the most stress-tolerant species of plant and micro-organism become dominant.

The evidence, discussed below, indicates that a feature crucial for the survival and growth of heathland plants in these most extreme soil environments is the presence of ericoid mycorrhizal infection. For convenience, the functional attributes of ericoid mycorrhizas can be divided into those providing direct benefits, most of which are nutritional, and those giving indirect benefits through detoxification.

It is fundamental to an understanding of the role of mycorrhizas in ecosystems to realize that the quality of the nutritional resources can be as important in determining their availability to plants as their quantity. This is nowhere better highlighted than in heathland environ-

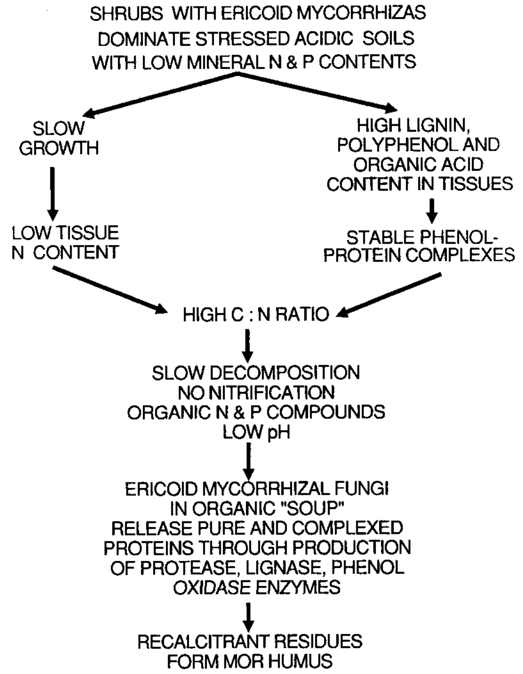

Figure 2. The major interactions between soil and plant in the heathland ecosystems indicating a central role for the ericoid mycorrhizal association in determining the success of ericaceous shrubs in these biomes.

ments, the soils of which are generally not impoverished because the *total* quantities of the major nutrients nitrogen (N) and phosporus (P) are low, but because these elements are in organic combinations which render them unavailable to autotrophs[137]. Rates of ammonification are low and nitrification is often inhibited completely.

Using sand cultures, early examinations of the biology of mycorrhiza in ericaceous plants indicated that the major benefits arose through enhanced nitrogen nutrition[116], in part by providing improved access to ammonium ions[138]. On the basis of these observations the higher tissue nitrogen concentrations might have been attributed simply to more effective capture of this relatively immobile mineral ion. However, experiments using heathland soil to which ^{15}N-labelled ammonium was added[137], showed that despite having significantly higher total nitrogen contents the proportion of the total attributable to the labelled ammonium ion was smaller than in uninfected plants.

This was the first indication that the mycorrhizal infection was providing access to a different type of nitrogen source. Since nitrate was not detectable in the soil, the only alternative source was the organic matter which typically contains 90–100% of the total N in soil surrounding ericoid roots. Analyses were therefore carried out on the relative abilities of mycorrhizal and non-mycorrhizal plants to utilize organic N sources. It was shown that infection provided access to amino acids[139], and that it also enabled the utilization of peptide[16], and protein[17] N. In no case was the uninfected plant able to utilize any of these substrates as an N source. Such observations necessitated a re-evaluation of the function of this type of mycorrhizal symbiosis. Clearly, infection was not simply improving the efficiency of absorption of those mineral ions which are of low mobility in soil, but was providing the capability to use an otherwise totally unavailable resource.

Understanding of the mechanisms of nutrient mobilization in the natural environment is dependent upon knowledge of the distribution of mycorrhizal roots in the soil. Studies in different heathland systems around the world[57, 111, 125] show that ericoid roots are densely packed in a zone close to the soil surface where they form a mat between the litter above and the humified material below. Even in situations where some of the roots do penetrate to greater depths, isotope studies have shown that the physiologically active component of the whole system is largely confined to the surface layers[20, 146].

The ericoid mycorrhizal infection is distinguished from the ecto and VA types in that the mycelium does not extend widely beyond the individual roots[117]. Hyphae spread outwards only for a few millimeters from the cortical cells to colonize the organic fragments surrounding the 'hair' roots. The architecture of the dense root system is, indeed, such that an extensive mycelium could do little to enhance exploitation of the small volumes of unoccupied domain in and around the root mat. The function of the mycelium in such a case cannot be to enhance capture and transport of minerals, a role for which the root system itself is admirably designed. Analysis of the biochemical potential of the mycorrhizal endophyte, *Hymenoscyphus ericae*, both in pure culture and in association with its host plants, suggests that it is equipped to play a quite different role. It has some ability to degrade chitin[86], lignin[72] and tannin[83] and hence has the potential to attack the structural components of the organic matrices at the base of the litter layer through which the roots are permeating. Such attack is likely to be a prerequisite for mobilization of the major nutrients nitrogen and phosphorus from the recalcitant residues of ericaceous plants (fig. 3) which is then achieved by the production of protease and phosphatase enzymes.

The protease of *H. ericae* has been identified as a carboxyproteinase of the pepsin type[84]. It has an optimum

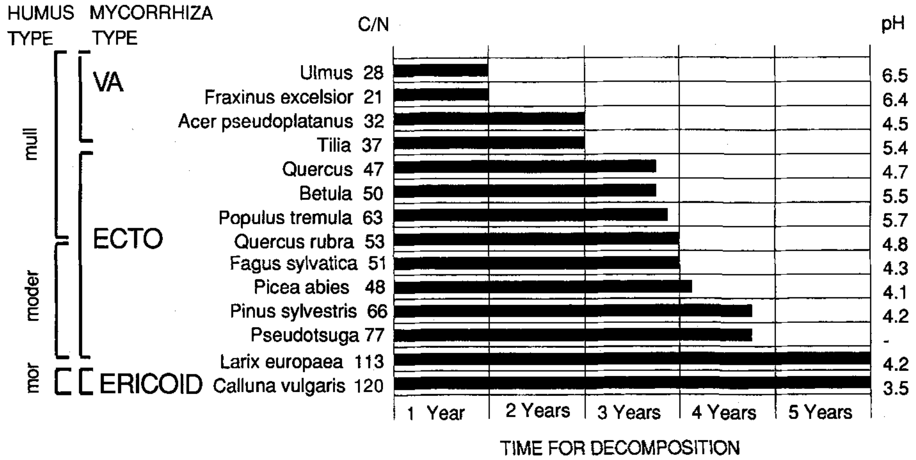

Figure 3. Inter-relationships between quality of litter (carbon: nitrogen [C/N] ratio, decomposition time, humus type and pH) produced by different tree species and the categories of mycorrhiza which have been selected to provide nutrient capture in each environment. Modified from Ellenberg[36].

pH for induction and activity between pH 2 and pH 4[85], which is in the range found in heathland soils. When grown with pure protein as sole source of nitrogen and carbon, *H. ericae* releases amino acids which are readily assimilated by the host plant without ammonification[123]. In attempts to simulate more closely the situation prevailing in heathland soil, studies of the ability of *H. ericae* to release nitrogen from proteins precipitated with tannin have shown[87] not only that the endophyte provides access to such proteins but also that the tannin is used to some extent as a carbon source.

We know less about the mobilization of phosphorus which, like nitrogen, is present largely in organic form in heathland soils. It has, however, been shown that the endophyte produces an acid phosphatase[108] and that it can utilize organic phosphates in the form of Ca, Fe and Al-phytates[98]. Characterization of alkaline, neutral and acid phosphatases of ericoid endophytes has been achieved by Straker and Mitchell[136]. Of these the acid phosphatase is most likely to be important in heathland soils. An ecologcally significant attribute of this enzyme is its resistance to inhibition by the metal ions Al^{3+} and Fe^{2+} both of which occur in solution at the pH prevailing in mor humus[131].

While low pH increases the threat of metal toxicity, the organic matrix can effectively chelate essential metal ion rendering them unavailable. The problem faced by organisms growing in acid organic soils is thus one of *regulation* of metal uptake rather than of capture or exclusion. Iron, an essential element which can also be toxic, is of particular interest in this respect. Schuler and Haselwandter[130] have reported the production by *H. ericae* of an iron specific hydroxamate siderophore and circumstantial evidence for the activity of such an iron chelating compound has been provided by Shaw et al.[132], who showed that mycorrhizal seedlings had a high affinity for iron when the element was provided at low external concentrations, a feature not shown by uninfected plants. Short-term assays of iron uptake by infected and uninfected plants revealed rates of Fe absorption of 3.9 and 1.8 nmol mg^{-1} d.wt h^{-1} respectively. When exposed to an excess of the element the high affinity mechanism is switched off but iron can be accumulated in the mycelium, where concentrations can reach 6 mg g^{-1} d.wt Fe, which thus provides a barrier to transfer into the shoots. A similar exclusion mechanism was demonstrated for zinc and copper ions which pose particular threats on some mine spoils[21, 22]. Metal exclusion provides sufficient resistance to permit growth of ericaceous species which, in many cases, are the sole colonists of such spoils. In addition to metal ions, organic acids pose a threat to would-be colonists of heathland raw humus particularly at low pH[75, 76, 113]. It has been demonstrated, however, that many of these acids are readily metabolized by the ericoid endophyte which can use them as a carbon source. As a result, whereas the roots of non-mycorrhizal ericaceous plants and of grasses fail to develop when exposed to mixtures of these compounds at ecologically realistic concentrations, those with ericoid infection proliferate freely. This demonstrates that the success of plants with ericoid mycorrhizas in some of the most stressed environments on earth is not attributable to their superior competitive abilities but to their ability, largely provided by the fungal endophyte, to tolerate the stresses.

The role of ectomycorrhizas in forest ecosystems

Below the alpine heath and tundra zones, trees of the families Betulaceae, Pinaceae, Fagaceae and Salicaceae form vast forests, covering much of Eurasia and North America, in which the main nutrient absorbing organ is the ectomycorrhiza. This type of association also occurs extensively in the Dipterocarpaceae and in some tribes of the Leguminoseae in the tropics, as well as in the Myrtaceae and Fagaceae in the Southern Hemisphere. It is necessary to seek features which might lead to the selection of this relatively uniform structure over such a wide range of environments.

As in the case of the ericoid mycorrhiza soil characteristics appear to be the key factor. The leaf litter produced by most of the ectomycorrhizal tree species while having a carbon:nitrogen ratio lower than that produced by ericaceous plants is still relatively slow to decompose and so forms a distinctive layer of acidic organically enriched material at the soil surface (figs 3 and 4). This is a feature of ectomycorrhizal forests whether they are of pine on

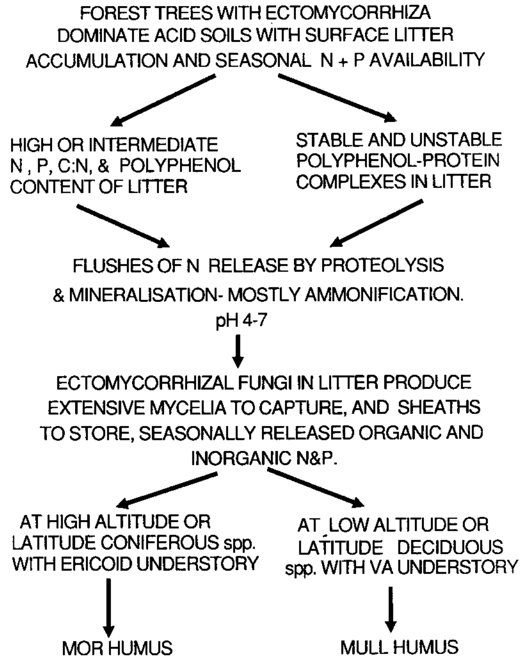

Figure 4. The major interactions between soil and plant in forest ecosystems dominated by ectomycorrhizal trees. These ecosystems span a broad spectrum of climate zones and hence have some characteristics of the heathland environment (see fig. 2) at one end of their range, and of the vesicular-arbuscular environment (see fig. 8) at the other.

impoverished sandy substrates[109], spruce or beech on mull soils or redzinas[36], or of tropical trees[6,101]. The quality of the organic matter developed from this litter varies from the most acidic raw humus or 'mor' on the poorest substrates, upon which plants with ericoid infection also often occur, through an intermediate 'moder' formed even over mull soils, to a mull humus over more base-rich substrates. The presence of this layer is evidence that mineralization processes are to some extent inhibited. Indeed, the rates of nitrogen mineralization of many forest litters are so slow that nitrogen characteristically becomes the key growth limiting element in these forests[15,36].

As in the case of heathland environments analysis of the distribution of mycorrhizal roots can provide vital clues as to their possible functional role. Detailed studies in boreal[71,105,109], temperate[67,97], subtropical[124], and tropical[6,101] forests have shown that ectomycorrhizas are concentrated in the surface layers where they are intimately associated with the litter. Since total amounts of the major nutrients in the litter layer can be high relative to those present in mineralized form, it appears that in these ecosystems, as in those dominated by ericaceous plants, it is the quality of the resource rather than its quantity which is of greatest importance. Acidity, high C:N ratio, and seasonality of climate with low temperatures and surface drying, are all likely to be major constraints upon mineralization.

The strong association between the occurrence of ectomycorrhizal roots and soils with organic surface horizons has led, from the time of Frank[52], to speculation that the ectomycorrhizal fungi were themselves directly involved in mobilization of the organic resources[88,92]. However, until recently the experimental evidence has supported the view that these fungi have limited ability to mobilize nutrients from complex polymers relative to that seen in fungi of saprotrophic habit[89,91,104]. While recent studies have largely confirmed that most ectomycorrhizal fungi, unlike their ericoid counterparts, fail to degrade the most complex polymers such as lignin[72,144], it has become increasingly clear that there is, in this group, a wider range of potential enzyme activity than previously realized. Thus, there is evidence in some ectomycorrhizal fungi of polyphenol-oxidase[56], cellulase[90] and some phosphatase[7,18] activities.

The ability of ectomycorrhizal roots to capture and store phosphate ions has been elegantly demonstrated[70], but since nitrogen is quantitatively the most important growth-limiting nutrient element in so many ectomycorrhizal forest systems it is likely that an ability to mobilize and capture this element will be of the greatest ecological significance. We now recognize that many of the most important ectomycorrhizal fungi of boreal and temperate forests, for example those in the genera *Amanita, Boletus, Paxillus, Piloderma, Suillus* and *Thelephora* produce a potent acid carboxypeptidase of a type similar in structure and major properties to that found in the ericoid endophyte. They thus have the potential to mobilize the growth-limiting nutrient, nitrogen, from protein[2]. The activity shows a pH optimum between 3 and 4 which is broadly representative of the range over which organic matter accumulates, and inhibition above pH 5.0[2,3]. The progressive replacement of ecto by VA-dominated plant communities in soils of pH above 5 can be seen as reflecting a loss in the selective advantage conferred by the biochemical potentials of the ectomycorrhizal fungi. The failure of Lundeberg[91] to detect significant amounts of proteolytic activity in ectomycorrhizal fungi is attributable to the fact that his assays were carried out at a pH 5.6, which is high enough to inhibit activity of these enzymes.

Studies of plants grown aseptically with and without their fungal associates have shown that only when in association with an appropriate fungal associate does the host have access to organic nitrogen[4]. This observation makes possible a reinterpretation of the function of ectomycorrhizas which have hitherto been seen simply as structures which improve the efficiency of capture of mineral nutrient ions.

It must be recognized that in addition to ectomycorrhizal fungi with high proteolytic capabilities, there are some, the so-called 'non-protein' fungi[2] that have little proteolytic potential. Amongst these *Laccaria laccata* and *Pisolithus tinctorius* are important examples. Such fungi are dependent upon mineralization processes, initiated by other organisms, for the release of N which is largely assimilated in the form of ammonium.

Further differences occur between the fungi in the effectiveness with which they transfer nitrogen, assimilated from protein, to their host plants. Thus, in studies using birch, it was shown that whereas *Paxillus involutus* and *Hebeloma crustuliniforme* showed comparable abilities to degrade protein, the latter transferred significantly more nitrogen to the host plant[3]. Trappe[143] stressed the fact that ectomycorrhizal forests and even individual trees were hosts to a great diversity of species of mycorrhizal fungi, and predicted that within this group there would be a comparable diversity of enzyme potentials. The experimental evidence relating to proteolytic capability supports this view and may help to explain some of the distinctive spatial and temporal patterns of distribution of ectomycorrhizal fungal species which have been reported.

In spatial terms ectomycorrhizal roots are food bases from which the fungal partner grows into a complex mosaic of organic substrates made up of qualitatively distinctive resource types. Mobilization of the critical nutrients in such a mosaic is likely to be enhanced by the specialized enzymic potentials of a number of fungi coexisting in adjacent or overlapping domains. Careful analyses of the distribution of the mycelia of different ectomycorrhizal fungi in sub-alpine forest soils[105] suggests the occurrence of just such a mosaic of resource types and of patterns of fungal colonization.

The use of transparent observation chambers containing unsterile natural substrates distributed in uniform or patchy manner has enabled the non-destructive analysis of the kinetics of growth and resource exploitation by ectomycorrhizal mycelia[23, 29, 38, 39]. The major strand-forming fungal species of ectomycorrhizal forests such as *Suillus bovinus, Amanita muscaria* and *Paxillus involutus* produce mycelia which grow in fan-shaped formation from infected roots. A diffuse mycelial front covers the substrate growing at rates between 2.4 and 5.6 mm per day. Behind the front, hyphal elements aggregate by collateral growth into linear organs, the 'strands' or 'cords', through which translocation occurs (fig. 5). The structure and development of these mycelial systems is comparable with that seen in many wood-rotting fungi[110]. The main difference between the two groups of fungi is that in the latter the food base is wood whereas the resource unit sought by the extending mycorrhizal mycelium is another mycorrhizal root.

The absence of host specifity in most ectomycorrhizal fungi means that their mycelia can form functional interconnections between their hosts at both inter- and intraspecific levels. In these systems, whether of single plants or groups, the ratio of total hyphal length to root length becomes progressively greater as the mycelial fan extends, being around 10^3:1 as development is initiated but increasing to 10^5:1 with time. Coutts and Nicoll[29] have shown that extension growth of such mycelia in *Thelephora terrestris* continues, albeit at a slower rate, even in winter.

Not surprisingly these mycelia constitute a major carbon drain upon the host. Using divided observation chambers in which the respiration rates of the intact mycelia could be measured independently of that of the host[140] it has been shown that mycelial respiration can be equivalent to 29% of that occurring in roots at the same temperature. This adds a new dimension to the already large estimate of the total allocation of carbon to below ground components of forest ecosystems. Some studies[48-50] have estimated that up to 50% of the total annual throughput of a Douglas fir stand can be accounted for by fungi, while others[145] suggest that around 15% of net primary production is consumed by the mycorrhizas. Harley[68, 69] calculated a likely carbon drain imposed by mycorrhizas upon trees of around 10%. None of these calcualtions took account of the external mycelium of the mycorrhizas.

The costs of establishing and maintaining these mycelial systems are so high that the returns obtained on the investment must be considered. The conventional view of the role of the fungal mycelium was that by growing beyond depletion zones around the roots it enhanced capture of phosphate ions. Structures such as those shown in figure 5 are clearly superbly adapted to such a nutrient scavenging function and there is evidence that phosphate[39], ammonium[40] and alanine[123] can be absorbed by the mycelium from forest soil and translocated through mycelial strands over considerable distances. These observations confirm those made under sterile conditions by Melin and Nilsson[94, 95]. Water can also be absorbed by the mycelium in quantities sufficient to maintain leaf turgor and photosynthesis under conditions in which the roots of the plant are in dry soil[23]. Because of the narrow diameters (ca 3 μm) of the individual hyphae making up the mycelium it is likely that only small fluxes of water can be maintained through each element. However, these conduits are present in such great numbers that, collectively, compensation for low fluxes through individual hyphae can readily be achieved.

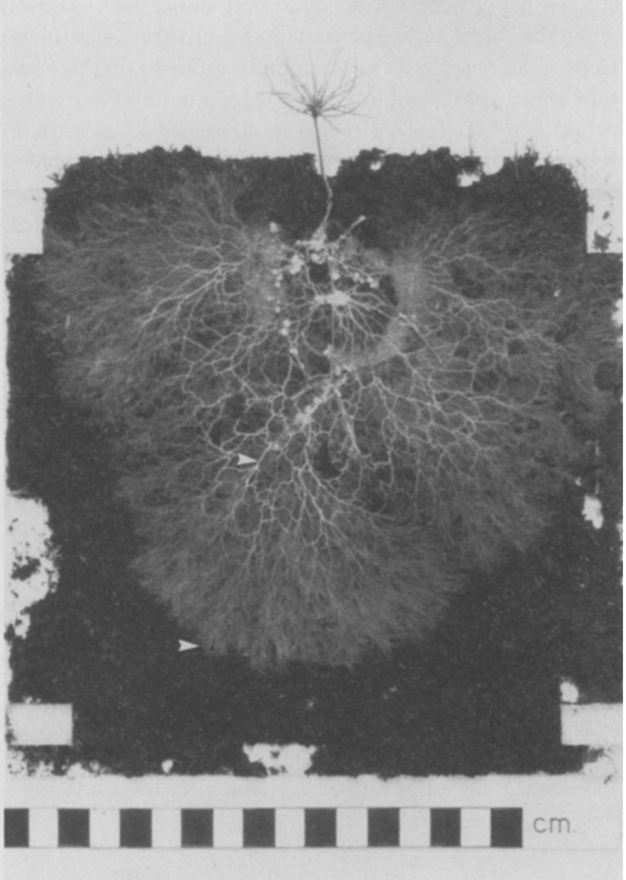

Figure 5. Seedling of *Pinus* infected with the ectomycorrhizal fungus *Suillus bovinus* and grown in an observation chamber on non-sterile forest soil. The effectiveness of the exploitation of the environment by the mycelial fan is clear. The mycelium is at an early stage of development but differentiation between the advancing hyphal front (lower arrow) and mycelial strands (upper arrow) is already evident. Mycelium: root length ratio is already 10^5:1 at this stage.

While being of considerable ecological interest, the fact that the mycelium fulfils absorptive functions leaves unanswered the more important question as to whether the fungi are directly involved in the mobilization of nitrogen and phosphorus from organic resources, so realizing in nature the potentials for phosphatase and protease production recognized in the laboratory. Increasingly, the evidence suggests that they are. Earlier studies using observation chambers indicated that even when the forest soil or peat used as a substrate was mixed to produce a resource of seemingly uniform quality, certain areas were more intensively exploited by the hyphae producing 'patches' of relatively dense mycelial growth. It was shown[38, 39] that these areas acted as sinks in which carbon, originally fed as $^{14}CO_2$ to the shoots of the host plant, and phosphate, fed as $^{32}PO_4$ to the hyphal front, accumulated. While attempts to induce such mycelial proliferation by localized application of mineral salts failed, addition of discrete blocks of partially decomposed leaf litter within the uniform matrix leads to 'patch' development (fig. 6). Evidence that this pattern of colonization was associated with nutrient absorption and transfer was provided first by the observation that chlorotic seedlings of *Pinus* and *Larix* rapidly became green as the blocks of organic matter were colonized. Subsequently it was shown that the re-greening of the host plant was associated with increases of the tissue nitrogen contents (fig. 7). It remains to be ascertained whether the mycorrhizal fungi are themselves mobilizing the resources, but the heavy investment of carbon and phosphorus in the patches is indicative of direct attack upon the substrates.

This pattern of proliferation of absorptive structures in localized areas of resource enrichment which has been called 'active foraging'[61] has been induced in the root systems of herbaceous plants[30, 34, 147] where it is associated with absorption of mineral ions. Intensive development of ectomycorrhizal mycelium in localized areas is a feature of natural forest soils. Large-scale examples of such exploitation are to be seen in the fungal wefts associated with the mycorrhizal roots proliferating in the decomposition horizons of coniferous forest soils[105], and in the mycelial mats formed by *Hysterangium* and related species underneath the organic horizons of Douglas fir forests[59, 60]. It has been estimated that the mycelium of *H. crassa* can occupy 9.6% of the A horizon of a forest soil to a depth of 10 cm[31]. These mats are known to be sites of elevated enzyme and respiratory activity[59, 60].

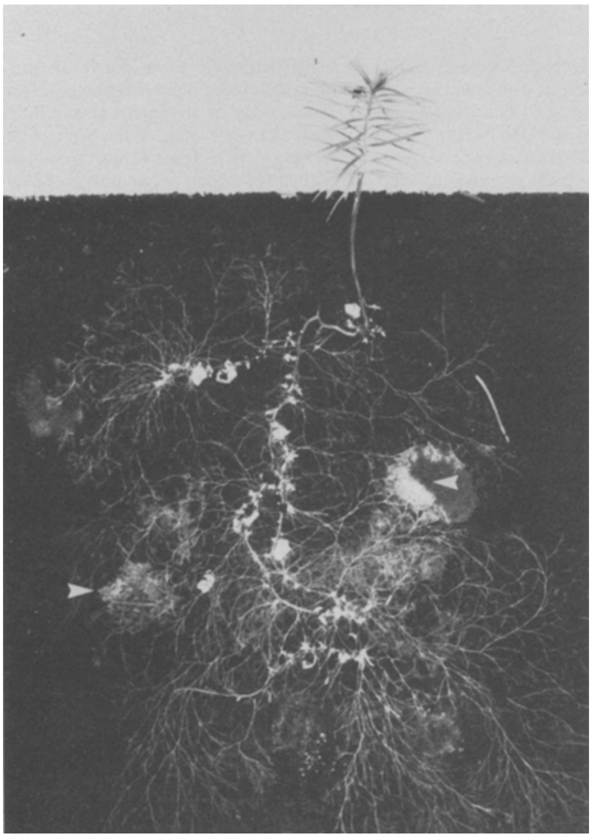

Figure 6. Induction of 'patch' development by introduction of leaf litter of larch (left arrow) or beech (right arrow) into an observation chamber containing a seedling of *Larix* infected with *Boletinus cavipes*.

In ectomycorrhizal forests the fungal mycelia themselves constitute a significant component of the total nitrogen source of the soil. Fogel and Hunt[49] calculated that the mycorrhizal sheaths of the trees contributed 50% or more of the total nitrogen inputs to a Douglas fir ecosystem. Similarly, Baath and Söderström[15] showed that in Swedish coniferous forest soils, up to 20% of the total nitrogen in a given horizon could be located in fungal mycelium. As these fungi senesce they will constitute a source of relatively labile organic nitrogen available for attack by the proteolytic enzymes of the living mycorrhizal mycelium.

The demonstration of proteolytic potential has necessitated a re-evaluation of the nitrogen cycle in the ectomycorrhizal forest ecosystem[123]. The infected trees are no longer envisaged as being entirely dependent upon the activities of a separate population of decomposers for the release of nitrogen in the form of ammonium ions. Through the provision of carbon to their own fungal partners they can themselves be involved in the primary mobilization events which, as studies in pure culture suggest, will lead to the release and assimilation of amino-compounds. The subsequent assimilation of these amino-

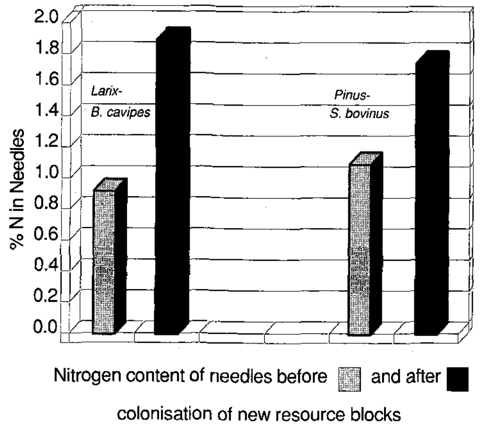

Figure 7. Changes of nitrogen concentration in leaves of larch and pine associated with 'patch' formation as their mycorrhizal fungi, *Boletinus cavipes* and *Suillus bovinus* respectively, intensively exploit introduced blocks of litter.

compounds in turn provides supplementary carbon as well as nitrogen to the host plant. In a study of assimilation of ^{14}C-labelled protein by mycorrhizal plants of *Betula pendula*, Abuzinadah and Read[5] showed that up to 9% of the carbon assimilated by the host plant over a period of 55 days was derived heterotrophically from the protein by way of its mycorrhizal fungi. It is likely that in nature the provision by the host plant of 'starter' carbon in the form of assimilate will enable the ectomycorrhizal fungi to compete successfully with other sections of the soil microbial community, the activities of which are normally carbon limited. Assimilation of products will subsequently reduce the demands upon host photosynthate and thus provide a positive feedback of carbon and nitrogen.

In temporal terms, successions of fungal species associated with ageing of forest stands have been reported by several workers[27, 33, 82, 93], and distinctions have been drawn between 'early-stage' and 'late-stage' fungi[32, 33]. Such successions are likely to be at least in part a consequence of changes in substrate quality as stands age and yield a progressive increase in the proportion of the nutrient fund that is in organic combination[58, 73]. This would be expected to select for fungi with the abilities to exploit such resources. The studies of proteolytic capability[2, 3] provide support for this view. All of the so-called 'late-stage' fungi examined so far have a well-developed proteolytic potential[2], and most have vigorous mycelial systems which are differentiated into strands. The situation with 'early-stage' fungi is less clear. Some of this category, notably *L. laccata* and *L. rufus* have little proteolytic potential while others such as *H. crustuliniforme* readily degrade protein. The vegetative mycelium of these fungi is, however, not differentiated into strands and it may be this feature of their biology rather than biochemical potential which restricts their ability to compete for food bases in older stands.

The distinction between 'early stage' and 'late stage' fungi is further blurred by the fact that in natural circumstances the 'late stage' fungi are the most vigorous colonists of seedlings. Fleming[45-47] found that young seedlings growing with mature trees in a birch wood were largely colonized by 'late-stage' fungi. A consequence of this mode of infection, which is likely to be of considerable ecological significance, is that young plants are rapidly integrated into the absorptive network of mycorrhizal mycelia. Detailed analyses at two woodland sites[103] have confirmed that seedlings of birch and oak developing under adult trees are infected almost exclusively by strand-forming fungi associated with these trees.

Uninfected root systems of seedlings of many tree species, but particularly of pine and spruce, are poorly adapted, both in terms of total length and branching pattern, to exploit the soil in which they develop. The benefits of infection by compatible fungi and hence of incorporation into the absorptive network can frequently be demonstrated in the form of increases in growth and nutrient composition[115]. Since such responses to infection occur in host plants at inter- as well as intra-specific levels, the incorporation into a compatible fungal network may form the basis of the well-known phenomenon of 'nursing'. Amaranthus and Perry[10] have observed that coniferous species often regenerate most successfully in association with those non-coniferous members of the community which are themselves ectomycorrhizal. Both the enhancement of growth of seedlings regenerating near adult plants and the stimulation of yield of some tree species when planted in 'mixtures', may be manifestations of the transfer of appropriate mycorrhizal associations from neighbouring plants.

The role of VA mycorrhizas in grassland ecosystems

Vegetation systems dominated by herbaceous plants with vesicular arbuscular mycorrhizas become progressively more extensive on a global scale as, with decreasing latitude, mean annual temperatures and evapo-transpiration rates increase. These changes lead to the reversal of the leaching tendencies prevalent in heath and many forest systems and to a consequent increase in base status and pH near the soil surface. As soil conditions are transformed there is an overall increase in numbers and activity of bacteria[96] which accelerate the turnover of organic matter and, more specifically, increase the propensity for nitrification. As a result the relatively mobile nitrate ion replaces organic matter and ammonium as the principal source of N for plants, nitrogen availability increases and the proportion of nitrophilous species in the community becomes greater. The litters produced by such plants have relatively low C:N ratios and they decompose rapidly (figs 3 and 8) so that the soils on which they grow have low organic contents. A most important feature of the changing nutrient status is that, as nitrogen turnover accelerates, phosphorus, the availability of which is reduced with increase of pH, becomes the major growth limiting nutrient. While this shift does not exclude ectomycorrhizal fungi completely, it signals a change towards conditions in which plants with VA mycorrhizas become dominant.

In contrast to ericoid and the majority of ectomycorrhizal fungi, the VA fungi appear to have a relatively restricted range of abilities to mobilize nutrients. However, laboratory studies confirm that they can provide infected plants with increased access to phosphate. This provision may result simply from the superior ability of the mycelium to exploit available soluble phosphate resources in soil[129], or from an ability, through the release of alkaline phosphatases[55] to solubilize unavailable pools of phosphorus[107]. Synergistic interactions between bacteria and VA fungi may also be important in facilitating phosphate mobilization in this type of soil[14]. Since, in nature, plants with VA mycorrhizas characteristically occur as heavily infected individuals growing in

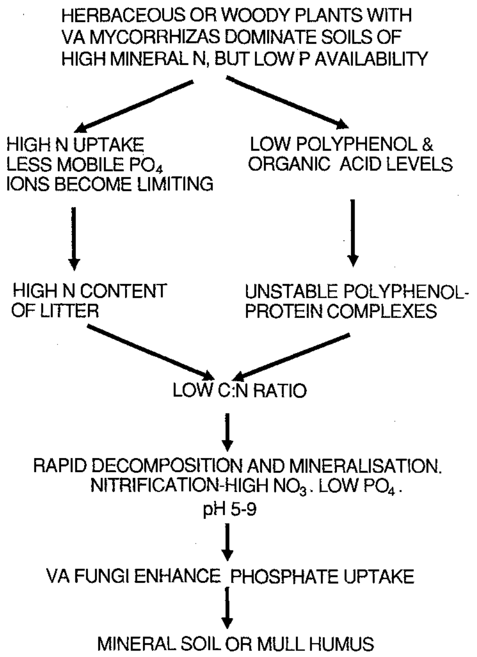

Figure 8. The major interaction between soil and plant in those ecosystems characteristics dominated by plants with vesicular-arbuscular mycorrhizas, identifying their central role in enhancement of phosphate uptake.

communities of mixed species[119], it is ultimately necessary to determine the role of infection in these circumstances. To date, most studies of intra- and inter-specific interactions have been carried out using simple combinations of plants growth together, with or without infection. Fitter[41] showed that the presence of infection changed the outcome of competitive interaction between two grass species. Similar results were obtained by Hall[65] and Buwalda[25] using mixtures of *Trifolium repens* and *Lolium perenne*. Infection improved the ability of *Trifolium* to compete with the grass especially when soil P contents were low. Dramatic effects of the presence of VA inoculum upon the outcome of competition between two prairie grasses *Andropogon gerardii* and *Koeleria pyramidata* have been reported[74]. *A. gerardii*, which was highly responsive to infection dominated when grown in the presence of inoculum, while *K. pyramidata*, a less responsive grass, was dominant in the absence of infection. Interpretation of the results of such experiments is made difficult because the fungal inoculum, often a monoculture of spores, may be more appropriate for one species than another and because the quantities of infection obtained are frequently much lower than those found in nature. Such problems are exposed in a recent study[35] of interactions between seedlings and larger plants of *Plantago lanceolata* when grown together in chambers. The seedlings grew poorly and acquired little phosphate when grown in the presence of larger plants irrespective of whether inoculum was added. The authors concluded that the principal interactions between the *P. lanceolata* plants were competitive and that the balance was not markedly altered by mycorrhiza. In their experiment, however, infection of seedlings was achieved not by the natural process of incorporation into an established mycelial network but by addition of inoculum in the form of root pieces at the time of seedling transfer. This may account for the fact that amounts of root length infected were less then 20%, in contrast to values seen in this species in the field which are normally between 50 and 90%[19, 102], and for the failure of the seedlings to respond to infection. It is vital when evaluating the function of mycorrhizas in natural ecosystems to facilitate the normal process of infection which enables the seedling root to become integrated into the extensive mycelial network already established by adult plants.

In natural and semi-natural ecosystems, seedling establishment takes place in small gaps or 'regeneration niches'[63] within communities of more mature plants, the roots of which already extensively and even exhaustively exploit the soil domain. It is at this stage in the development of the plant that the impact of VA infection is first seen. Harvesting of seedlings from the field situation has revealed that infection takes place at an early stage in their development[44, 54, 119]. It was predicted[119] that early integration of the seedling radicle into the mycelial network would, as in the case of ectomycorrhizal systems, provide the plant with an enormous increase in absorptive surface at relatively low energy cost, thus giving it access to resources otherwise tapped exclusively by the established plants. The infection process was thus seen to be of potentially profound importance not only for the individual plant but, through effects upon recruitment of seedlings, upon the structure of the community as a whole. Subsequent studies have largely confirmed these predictions. The process of infection development has been quantified[19, 118] by planting seeds of the dominant species of calcareous grassland onto the undisturbed soil surface in the field at the time of radicle emergence.

Infection takes place within three days in the axial root and 4.3 days in the laterals. The spread of infection in the root can, however, be slow, individual blocks of mycelium extending at a rate of only 0.1 mm day $^{-1}$.

In the field, therefore, new penetrations must be the dominant mechanism of infection spread. This in turn means that the internal mycorrhizal structures of the host root are directly connected to the external mycelial network at frequent intervals. Counts of penetration points confirmed the intimacy of contact between root and mycelium in the soil, values of up to 100 entry points cm^{-1} of root being obtained[133].

Analysis of arbuscule development in these roots revealed that the median time from root penetration to arbuscule formation was 1.3 days. Brundrett et al.[24] obtained similar results but in older roots. Since these are the structures through which phosphorus passes to the plant, their presence at this stage of the infection process suggests that mycorrhizas are functionally active very soon after penetration. However, arbuscules are known to have a short life-span, slow senescence being observed from 4 days after formation[142]. Their ability to contribute phosphorus to the root will therefore be determined by the size of the resource to which they are attached outside the root and by the speed with which this can be mobilized. Here the contrast between spores or root fragments, and the intact mycelial network, as sources of inoculum, is highlighted. Whereas the total P content of a spore or fragment of root is finite and its mobilization will be dependent upon investment of carbon from the newly-infected plant, those hyphae penetrating from the mycelial network are part of an enormous catchment with a large absorptive surface, the carbon requirements of which can be met by surrounding established plants.

In nature, it seems that significant inflows of P do occur soon after infection. By determining the ratios of phosphorus to nitrogen (P:N) in shoots of seedlings in the course of sequential harvesting for infection assessment, Read and Birch[118] showed that after an initial fall, presumably as seed reserves of P were used, P:N ratio stabilized as infection developed. In the cases of *Festuca ovina* and *Plantago lanceolata*, the P:N ratio stopped falling at the time of appearance of the first infections in the lateral roots.

Direct evidence for the presence of physiologically functional VA hyphal interconnections in intra- or interspecific combinations of plants has been achieved by means of autoradiographic analysis of intact systems, in which plants, which had also been the source of infection for associated seedlings, were fed with $^{14}CO_2$[51,120]. Radioactivity was seen to accumulate in the external mycorrhizal mycelium and to be transferred through hyphae penetrating the roots of 'receiver' plants to the vesicles or arbuscules forming in those plants. Subsequent quantification of this radioactivity revealed that more transfer occurred into shaded than into fully illuminated plants, suggesting that transfer processes are determined by source-sink relationships.

Many studies of the development of VA infection have been based upon the use of dispersed propagules in the form of spores, mycelia or root fragments. The cultivation of agricultural soils will produce such fragmentation and dispersal of propagules, but the negative impact of these procedures on the infection process is increasingly recognized. Tillage of soil prior to planting of maize has been shown to lead to considerable reduction of infection intensity and nutrient inflow, which can be attributable directly to impacts of disturbance upon the mycorrhizal mycelium[36,106]. There is evidence that detachment of VA hyphae from their food bases leads to reduction of inoculum potential. It has been shown that following disturbance of small patches of soil within natural grassland the numbers of penetrations of seedling roots was little affected but the vigour of the infection within the roots was significantly diminished[118]. Jasper et al.[79] carried out a more drastic disturbance in pots of soil containing a mycelial network which had previously been detached from its host plant. This network retained vigorous infectivity for several days if it was intact, but when the soil was extensively disturbed by chopping and mixing infections were eliminated. In a further study of great ecological interest the interaction between infectivity of the hyphal network and drought was examined[80]. This experiment showed that, providing the mycelial network was left intact after it was separated from the host roots, its infectivity was retained for at least 36 days even when exposed to soil water potentials as low as −21 M Pa. These results are of importance to an understanding of the dynamics of plant communities in seasonally dry climates because they suggest that roots developing after the first rains will be rapidly infected and hence able to benefit maximally from the flushes of nutrient release known to occur at these times. Conversely, it was shown that disturbance of the network in dry soil leads to a reduction of its inoculum potential[80] which helps to explain the loss of infectivity seen when soil is disturbed and dried, for whatever reason[78,126].

These observations raise a further but hitherto controversial aspect of the ecological function of VA mycorrhizas, namely their ability to enhance water supply to the host in the characteristically drought prone habitats which they dominate. Studies using plants grown in petri dishes with only about 6 hyphal entry points per cm of infected root length have led to the suggestion that rates of transfer of water through hyphae were too small to contribute significantly to transpiration of plants[28]. However, in nature plants frequently have between 20 and 200 entry points per cm of root so that the total fluxes of water to large root systems can be much greater than those determined under laboratory conditions[121]. It is known that breakage of hyphal connections leads to rapid fall of transpiration rate[56]. Recently also, the frequently stated view that any increased water throughput associated with VA infection was only a secondary product of enhanced access to phosphate[9,100,127,128] has been challenged by studies which clearly demonstrate greater transpiration rates in infected plants which are of comparable size and P status to those which are uninfected[11,12].

In studies of the impact of mycorrhizal infection upon the water relations of two grasses of xeric habitats, it has been shown[8] that one of the species *Agropyron smithii* had lower stomatal resistance and increased leaf water potential when infected, but only during the driest part of the growing season. Low stomatal resistance was maintained in infected plants of this species even when it was grown in competition with annuals. These workers postulate that under field conditions mycorrhizal infection is of importance under particular circumstances of stress which were described as 'ecological crunches'. Such results again emphasize the need to assess the role of mycorrhizas over the life of the plant, rather than over a short period of time at some stage after establishment or between episodes of stress.

In an attempt to investigate the role of VA mycorrhizas at the community level, Grime et al.[62] employed microcosms in which ecologically realistic assemblages of herbaceous plants were allowed to develop with or without the presence of mycorrhizal fungi. This mixture which was sown within a matrix of seedlings of the grass *Festuca ovina* included species which are known not to be normally susceptible to mycorrhizal infection. The communities were harvested after 12 months. Immediately prior to harvesting, $^{14}CO_2$ was fed to shoots of *Festuca* in selected microcosms and the pattern of distribution of label was determined. Transfer of radioactivity occurred almost exclusively in the microcosms containing mycorrhizal fungi and in these only to plant species which were actually infected. These observations provide further evidence that plants in natural communities are functionally interconnected by their mycorrhizal fungi. Determination of dry weight of the individual species from each microcosm showed that the presence of mycorrhizal infection caused a shift in the distribution of biomass from the dominant *Festuca ovina* in favour of subordinate species. Those forbs with small seeds which were receptive to infection benefiting most from the presence of VA fungi. The effect was to produce a significant increase of species diversity in the inoculated microcosms. Such results indicate that the characteristic diversity of species found in so many communities dominated by plants with VA infection may be attributable to the presence of the fungal associates which facilitate nutrient capture by the most vulnerable species at a critical phase in their life cycle.

It is obviously desirable to extend such studies to the field but the difficulties involved in interpreting results of experimental manipulation of mycorrhizal infection in the field are immense. Since a prerequisite of such experimentation is the need to compare blocks of vegetation with and without the presence of mycorrhizas, a soil treatment is needed that is sufficiently selective to eliminate mycorrhizal fungi while having little effect upon the rest of the microbial community or upon the nutrient status of the treated block. No such treatment is available. This explains why most experiments designed to test the effectiveness of VA mycorrhizal infection in the field have produced inconclusive results[42]. Sterilization of soil by whatever means inevitably influences the nutrient balance, and these effects become progressively larger with increasing proportions of soil organic matter. Attempts to manipulate the mycorrhizal population using the partially selective systemic fungicide benomyl have produced inconsistent results. Application of benomyl to established vegetation can reduce[43] or have no effect[81] upon infection. When infection is reduced there may be no impact upon tissue nutrient concentrations[43]. Since benomyl may have adverse effects upon fungal species that are antagonistic to mycorrhizal fungi[141] its impacts will inevitably be unpredictable.

Other factors combine to reduce the likelihood that application of fungicides to established vegetation systems will provide a sufficiently sensitive means of determining the function of mycorrhizas in ecosystems. Foremost among these is the fact that the nutrient dynamics of those plant communities growing on infertile soils which are most susceptible to mycorrhizal infection, are characterized by seasonal pulses of nutrient mobilization rather than continuous release[1,64], and by an uncoupling of resource capture from growth[26]. In these circumstances the mycorrhizal network will facilitate capture and transport of the released resources which can subsequently be stored in the fungal or host tissues for use during periods between nutrient flushes. It is the essential conservatism of the nutrient economies of those ecosystems most dependent upon mycorrhizal infection which makes them least likely to respond to short-term application of fungicide.

If as predicted earlier, VA infection plays a crucial role at the time of seedling establishment, then a more promising approach is to eliminate mycorrhiza at the start of, or during the early stages of, a secondary succession. Such an approach has recently been employed[53]. A non-systemic fungicide ‘Rovral’ (iprodione) was applied to blocks of soil which had previously been cleared of plants, raked and harrowed. The subsequent successional processes were compared with those occurring in untreated soil. The study showed that species richness and total cover abundance (fig. 9), were significantly decreased by the application of the fungicide. Of the six species of forb which showed significant reduction of infection as a result of fungicide application four, *Tripleurospermum inodorum*, *Veronica persica*, *Vicia tetrasperma* and *Medicago lupulina*, also showed a significant reduction in their cover abundance. These trends, which are broadly comparable with those obtained in microcosms after one year's growth[62] are particularly noteworthy because they were obtained after disturbance which was likely to have reduced the inoculum potential and so provided an underestimate of the mycorrhizal role.

Summary and conclusions

The emerging evidence points to the likelihood that the major role of the distinctive mycorrhizal symbioses in the various terrestrial biomes is to provide plants with access to key growth-limiting nutrients at crucial stages in their development. On a global scale the differentiation between biomes dominated by plant species with VA, ecto- or ericoid mycorrhiza occurs along a gradient of increasing accumulation of organic matter which essentially involves major changes in the quality rather than the quantity of nutrient resources. The associated increases in the ratios of C:N and C:P inevitably lead to greater recalcitrance of the mineral nutrients and to development of selection pressures favouring mutualistic associations be-

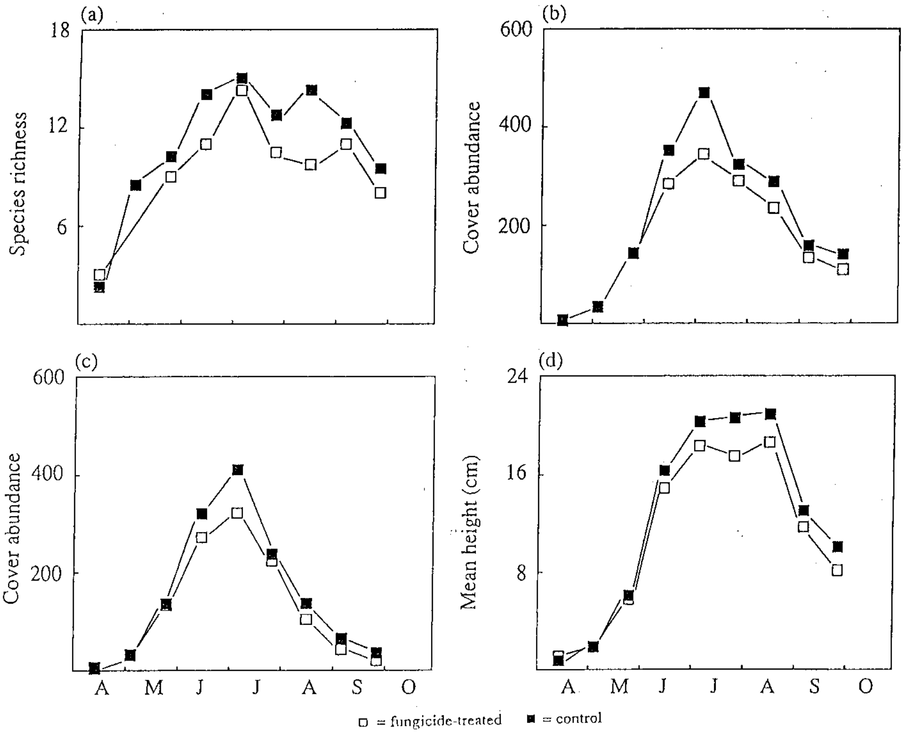

Figure 9. The effect of removal of mycorrhizal inoculum, by application of fungicide, upon processes of plant community development during the first year of colonization of bare ground. (a) species richness (mean per plot); (b) cover abundance; (c) cover abundance of annuals forbs; (d) sward height. Reproduced from Gange et al.[53] with permission.

tween plants and specialized heterotrophic partners which have access to the key resources. It is likely that such pressures have made a major contribution to the segregation of mycorrhizal types and their respective biomes into the distinctive zones recognized in figure 1. Recognition that nutritional niches can be differentiated in terms of quality as well as quantity is likely to be of importance for ecologists who widely assume that plants compete for the same, essentially mineral, nutrient resources. Niche differentiation based upon the use of distinct nutrient resources will enable plants to co-exist in the absence of significant competition for nutrients. It also may help to explain the occurrence, in transitional areas of the global gradient, of mixtures of ericoid and ectomycorrhizal species or of ecto- and VA species. However, even in these areas, the qualitatively distinct resource types are often spatially separated. For example, where a litter-layer overlies a mineral or lateritic soil, ectomycorrhizal roots may exploit the organic horizons while the mineral soil is occupied by roots with VA mycorrhizas[124].

Analyses at the global scale suggest that climate, through its effects upon soil development, is of primary importance in influencing the type of mycorrhizal community formed. Studies at the local level, however, readily demonstrate that changes in the quality of soil nutrient resource, brought about by whatever means, are of primary importance and that climate is, at most, a secondary factor.

Thus in sand dune ecosystems progression over short distances from disturbed strand-line situations through young mobile and semi-stable to older stable dune soils, involves steep gradients of decreasing pH, increasing organic accumulation and of changing mycorrhizal type. Non-mycorrhizal ruderal species at the strand-line are replaced first by those having facultative associations with VA fungi, these in turn being replaced in stable dunes by plants which are highly responsive to VA infection. With accumulation of organic matter as dune soils age ectomycorrhizal species appear and, eventually, in the oldest and most acidic parts of the system species with ericoid mycorrhiza can predominate[122].

A similar sequence appears to occur in many other successional environments suggesting again that mycorrhizal infection plays a central role in determining the types of plant community predominating at any stage of the succession. That many species of the later stages of succession in tropical rain forest are dependent upon VA infection is known[77]. However, even within what appears to be climax vegetation, local changes of edaphic conditions can lead to the development of plant communities which are distinctive both in terms of species composition and mycorrhizal type. In the tropical rain forest of Cameroon groves of ectomycorrhizal caesalpinoid legumes occur within an ecosystem otherwise dominated by trees with VA mycorrhizas in areas in which soil is of low mineral availability and increased surface organic content[101]. Again, therefore, compatibility with appropriate mycorrhizal associates appears to be a key factor determining not just the fitness of the plants but the structure of the whole plant community.

The first century of research on mycorrhizas has provided description of the major types of infection and a careful, largely laboratory-based, analysis of their function. We now enter a new phase in which the challenge is to evaluate the function of the symbiosis in the real world. The difficulties involved will be great but the evidence obtained so far suggests that the rewards obtained in terms of understanding of ecosystem function will justify the effort.

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0014-4754/91/040376-16$1.50 + 0.20/0

The significance of mycorrhizas for protective ecosystems

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Summary. On the basis of the reviews presented in this issue, the ecological significance of mycorrhizal symbioses is discussed. Mycorrhizas may have some importance in the acquisition of mineral nutrients during the productive phase of ecosystems in early stages of succession, but their main role is played during the protective phase of ecosystems in the final stages of succession when most resources are incorporated into biomass. In these successional stages, mycorrhizas short-circuit nutrient cycles by directly reacquiring nutrients in organic form from plant (and fungal) litter, and they may reallocate resources between different plant individuals, preventing loss of resources from the entire ecosystem.

Key words. Ecosystem; mycorrhiza; symbiosis.

Introduction: Productive and protective ecosystems

The entire biomass on earth, if it were spread evenly over the planet's surface, would form a thin film of less than 1 mm in thickness[14]. The living organisms forming this biomass render the earth hospitable because they do not occur in an isolated film, but interact with the atmosphere, hydrosphere and lithosphere, generating climate and soil[14]. In this way, the biosphere can be considered to be a web of dynamic interactive structures, powered by solar energy, with their own laws of space and time, of stability and change.

Today, the biosphere is in danger in two senses: directly, through outright destruction and through the monopolization of many areas for 'productive' use with single plant or animal species according to criteria of maximal yield; and indirectly, through the burden of waste transferred for disposal from the destroyed or 'productive' areas to the shrinking 'unproductive' areas, a burden that may overload the protective capacities of these areas[22]. This consideration brings the endangered *protective ecosystems*[22] into focus. Some people may think that such protective ecosystems may be investigated and 'rationalized' with the same approaches that promoted progress in *productive ecosystems*. However, we concur with Odum[22] that protective and productive ecosystems are different and cannot be approached in the same way, as illustrated in the following comparison of their properties.

Productive ecosystems, typical of pioneer stages in secondary successions, are characterized by the rapid transformation of environmental resources (light, carbon dioxide, water, mineral nutrients) into biomass. This includes rapid uptake and assimilation of nutrients from soil. Ruderals are well adapted to the conditions of productive ecosystems, which include high availability of nutrients from the soil as well as a high frequency of disturbance. Most crop plants have been developed by breeding from ruderals, since arable land is subject to the same set of conditions[3], and the principal aim of crop breeding consists in improving the already preadapted strategy of ruderal plants to grow rapidly and to mature quickly on the basis of abundant mineral resources. In contrast, protective ecosystems, typical of the terminal stages of succession leading to the climax, have incorporated most of the available mineral resources into biomass and use the remaining resources (light, carbon dioxide, and water) mainly for maintenance and protection from perturbations[22]. They contain long-living plants which grow slowly, set fruit after a long juvenile period, frequently coexist with a large number of other species, and create, control, and stabilize to a large extent their own microclimate and soil conditions. In these ecosystems, acquisition of mineral nutrients from the soil is of little importance in comparison to the recycling of nutrients within the existing biomass, preferentially in closed cycles with little loss[11]. Hence, productive and