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Acquisition of nutrients from organic resources by mycorrhizal autotrophic plants

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Summary. Evidence exists to suggest that mycorrhizal fungi are capable of producing enzymes allowing them to access carbon, nitrogen and phosphorus from complex organic resources in soil. This facility is mainly demonstrated in ectomycorrhizal and ericaceous endomycorrhizal fungi associated with highly organic soils and climatically stressed environments. These data support a direct nutrient cycling hypothesis proposed for tropical ectomycorrhizal forests. In terms of forest succession, the evidence agrees with a major contribution of the mycorrhizal symbiosis in late stages of the succession, where elemental cycling becomes increasingly more conservative and process rates limited by biotic factors. Here, tree growth benefits from direct nutrient cycling mediated by their mycorrhizal symbionts.
Key words. Direct cycling; phosphatase; phytase; enzymes; succession; decomposition.

Introduction

Soils are derived from parent rock by the processes of erosion by wind, water, temperature change and the effects of plant roots. Essential plant mineral nutrients are dissolved from the parent material and the whole provides a structural and nutritional resource on which autotrophic plants may survive. Through the fixation of carbon by photosynthesis, carbon is added to the soil in complex forms with mineral nutrients (nitrogen, phosphorus, sulphur, calcium, etc.) as plant litter, either by the shedding of plant parts or in the death of the plant. Soil is the home of many animals (arthropods, nematodes and earthworms) which, together with fungi and bacteria, are involved in the breakdown of these organic resources, using the carbon as an energy source and remobilizing mineral elements into the soil solution. The dead bodies and exudates from these animals also contribute to the organic content of soil. Soil is thus a highly heterogenous medium in which the processes of nutrient immobilization and mineralization occur, resulting in pools of inorganic nutrients in solution which are available for uptake by plant roots[19]. Taking a simplistic view, the role of mycorrhizal fungi is to enhance the plant root's ability to capture dissolved mineral nutrients from the soil solution before they can either be immobilized into tissues of other organisms (fungi, bacteria or competing root systems) or are leached down the soil profile beyond the physical extent of the rooting system. Mycorrhizas are thought to do this by increasing the surface area of the root, thereby extending the nutrient depletion zone further from the root surface (see reviews by Fitter and Hetrick in this issue). A general concept of soil nutrient cycling, as outlined above, is presented in figure 1. In 1968, however, Went and Stark[79] proposed a more direct nutrient cycling system based on their observations of tropical forest soils. They noticed very close associations between ectomycorrhizal roots and their fungal hy-

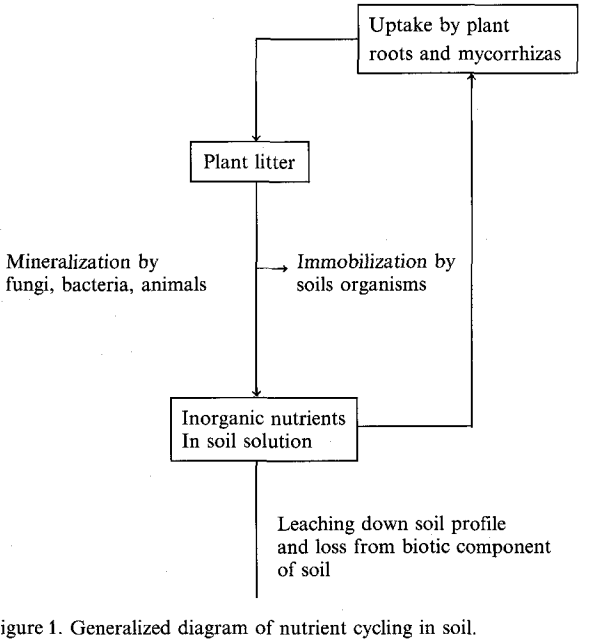

Figure 1. Generalized diagram of nutrient cycling in soil.

phae and organic resources in sandy tropical soils. Their three main observations were as follows: 1) woody fruits were readily penetrated by hyphae in the region of mycorrhizal roots; 2) mycelium and roots were confined to the litter layers; and 3) tree stumps which were not invaded by mycorrhizal roots bore fruitbodies of wood rotting fungi of the Polyporaceae, *Xylaria*, etc., whereas in the presence of ectomycorrhizal root invasion of the stump, no fruitbodies were produced (potential competition between mycorrhizal and saprotrophic fungi). On the basis of these observations, they hypothesised the involvement of mycorrhizal fungi in a saprotrophic function which allowed these fungi to obtain nutrients for their host directly from organic resources in the soil (fig. 2).

In order for mycorrhizal fungi to play a role in the direct cycling of nutrients from complex organic resources in soil to their host plant, the fungi need to have the ability to produce the appropriate enzymes and to be able to compete with saprotrophic fungi for the resource unit. This facility would, naturally, be of greatest importance in areas where the organic components of the soil were most important.

The potential for direct nutrient cycling

Accumulation of organic matter in soil is a function of resource quality[32, 33, 68], i.e. the ability of the litter to be broken down, and climatic conditions. Decomposition is usually favoured by warm moist conditions and inhibited by cold and dry conditions. Read[63] summarized the changes in vegetation, soil organic matter accumulation and mycorrhizas on both an altitudinal and latitudinal gradient. His scheme shows that as one ascends in altitude or progresses towards the poles from the equator, in general one moves from soils which are mainly inorganic (due to rapid decomposition and nutrient cycling) through soils of increasing organic matter content (due to slower decomposition) to very poor, shallow and mainly inorganic soils (due to limited plant productivity in climatically adverse conditions at extreme altitude or close to the poles). Vegetation changes with increasing organic matter accumulation from herbaceous plants through deciduous, mixed and coniferous forests to ericaceous vegetation on the deepest organic soils. Consequent changes in mycorrhizal flora are from vesicular-arbuscular mycorrhizas through the ectomycorrhizas to the ericaceous mycorrhizas. Thus, it is expected that the ability of mycorrhizas to degrade organic matter and become involved in direct cycling of nutrients is of major significance in the ectomycorrhizal and ericaceous mycorrhizal dominated communities.

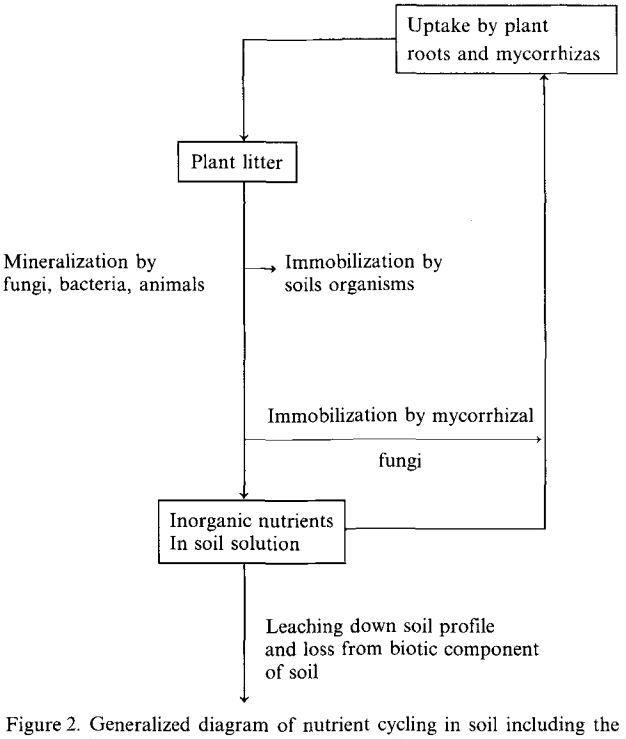

Figure 2. Generalized diagram of nutrient cycling in soil including the direct cycling of nutrients from organic complexes to plants.

In an article on the occurrence of basidiomycete fungal fruitbodies in beech forests in Sweden, Tyler[77] showed, from 300 permanent observation points over 5 years, that the frequency of occurrence of mycorrhizal fungi was greater in soils of high organic matter content and lower metal ion saturation. Saprotrophic fungi were more common in soils of lower organic matter content and higher metal ion saturation. This evidence suggests that there may be a role of mycorrhizal fungi in decomposition of organic matter or that their presence is required to a greater degree where the rate of mineralization of nutrients is lower. Here, they may compete with the saprotrophs for mineralized nutrients, resulting in the inability of the saprotrophs to produce fruitbodies.

Within communities of ectomycorrhizal plants, changes in nutrient dynamics in forest soils with succession may also be important in altering the balance of nutrient supply by the soil and demand by the tree. Where supply is lower than demand, direct nutrient cycling by mycorrhizal fungi would be of great benefit to the host tree. As forest succession advances, essential nutrient elements become locked up and conserved in the ecosystem in both tree biomass and soil organic matter[33, 78]. As the forest reaches canopy closure, when the tree canopies overlap, there is light reduction on the forest floor inhibiting growth of herbaceous plants. The forest loses the input of readily degradable litter from these plants and there is an increase in accumulation of recalcitrant, tree-derived litter on the forest floor. At this time, tree growth is maximal and there is an imbalance between nutrient supply and demand[56, 75, 76] which has recently been demonstrated for phosphorus, using a root bioassay[18, 20]. In the mature forest, increased nutrient cycling within the tree[26], and increased mineralization in the forest floor redresses the former imbalance.

Evidence from fruitbody observations under birch trees of increasing age[53, 54] suggests there are successions of

ectomycorrhizal fungal species. Similarly, in forests of *Pinus radiata*[14], *Pseudotsuga menziesii*[15] and *Pinus contorta* and *Picea sitchensis*[22] there is evidence of changes in dominant ectomycorrhizal species and species richness (diversity) with forest succession. Maximum species diversity was found to occur around canopy closure when the organic nutrient capital of a forest soil is maximal. The rate of mineralization of nutrients from this important resource is a limiting factor for tree growth. This hypothesis has been explored in the reviews of Dighton and Mason[21] and Last et al.[45] in relation to changes in the physiology and habit of mycorrhizal fungi as predicted from 'r-'- 'K-'strategy theory sensu MacArthur and Wilson[51]. As succession advances 'r-'strategists, which are ephemeral, opportunistic species surviving by virtue of competition by rapid growth, low energy investment in biomass and production of many, readily germinable propagules, give way to 'K-'strategists. These are slower growing and compete by the production of antagonistic factors, invest energy into long-lived, structured biomass with greater physiological diversity and produce fewer propagules which have a higher chance of survival. It is to these 'K-'strategists among mycorrhizal fungi that one must look for the enzymatic competence to act as saprotrophs (fig. 3). Alternatively, in extreme environmental conditions, stress tolerant species ('S-'strategists, sensu Grime[30]) may also possess these characteristics.

Is there evidence to support a direct nutrient cycling theory?

The general hypthesis proposed by Went and Stark[79] for tropical forests has never truly been proved or disproved. Singer and Araujo[65] support the view of Went and Stark, suggesting that in the Amazonian forests direct cycling of phosphorus from litter would not occur in latosol-terra-firma soils where mineral phosphorus is adequate for tree growth but would possibly occur in the ectotrophic forest on white podzol campinarana where soluble inorganic phosphorus is less readily available. However, no direct evidence is supplied. In his discussions on tropical forests dominated by VAM (vesicular-arbuscular mycorrhiza), Janos[37,38] states that obligate mycorrhizal associations occur on soils with low mineral nutrient availability and that these sites are dominated by ectomycorrhizas under low tree species diversity because of the specificity of the association and the highly beneficial nature (unspecified) of the fungal association. Janos, however, suggests that it is probably the close proximity of mycorrhizal hyphae to sites of nutrient mineralization which confer an advantage to ectomycorrhizal trees rather than involving the need for saprotrophic function in the mycorrhizal fungi themselves. This is a view shared by Trappe and Fogel[73] who suggest that, apart from orchidaceous mycorrhizas, mycorrhizal fungi possess little or no saprotrophic ability. Lindeberg's[48] comments that mycorrhizal fungi show little ability to produce extracellular enzymes, e.g. cellulase, pectinase, proteinase and laccase also support this idea. He quotes from Lindeberg: "Because mycorrhizal fungi do not depend on litter for their carbon and energy, they compete successfully with litter decomposing fungi for available inorganic nutrients. The effectiveness of the nitrogen uptake of the mycorrhizal fungi probably contributes to the prevention of leakage of nitrogen from the forest ecosystem".

The quote derives much of its origin from experiments carried out in the 1970s by Gadgil and Gadgil[27,28]. They suggested that the presence of mycorrhizal roots in organic layers of soil suppressed litter decomposition. In a field experiment in a *Pinus radiata* forest (summarized in table 1) they manipulated the rooting conditions of isolated blocks of soil in the field in which litter was present. Undisturbed soil blocks (i.e. root zone intact) resulted in least loss of litter weight and where the soil block had been isolated by cutting at the edges and the soil dug or dug and roots removed, the greatest litter weight loss occurred. Similarly, in a laboratory experiment, *Pinus radiata* plants were inoculated with forest soil organic matter (duff) potted into perlite/sterile duff medium with litter added to the surface (table 1). Again, where mycorrhizal roots were present, the litter weight loss was reduced. Where saprotrophic fungi were deliberately add-

	Stage of development of forest →		
	Young	Canopy closure	Mature
Litter layer	Thin herbaceous litter – decomposes rapidly.	Thick – tree derived litter – recalcitrant to decomposition	
Inorganic nutrient status	Nutrient supply exceeds tree demand	Tree demand exceeds nutrient supply	Nutrient supply and demand are approximately in balance due to internal recycling in tree
Mycorrhizal fungal species diversity	Low	High	Low
Mycorrhizal attributes	Efficient scavengers for inorganic nutrients	Act as decomposers – direct cycling of nutrients	Act as decomposers or work in synergism with saprotrophs

Figure 3. Key stages in forest development invoking the role of saprotrophic abilities in ectomycorrhizal fungi.

Table 1. Effects of manipulating field (a) and pot culture (b) conditions to show the effect of mycorrhizal *Pinus radiata* roots on decomposition of litter (after Gadgil and Gadgil, 1975)[28].

(a)	Treatment	Litter dry weight as % of control after 1 y
	Control – litter removed and replaced	100
	Block cut, litter removed and replaced	44.8
	Block cut, dug to 30 cm depth, litter removed and replaced	42.2
	Block cut, dug, roots removed, litter removed and replaced	63.5
(b)	Treatment	% litter weight loss after 6 mths
	Mycorrhizal plant + saprotrophs	39.4
	Non-mycorrhizal plant + saprotrophs	44.0
	No plant + saprotrophs	43.4
	Mycorrhizal plant	44.2
	Non-mycorrhizal plant	49.9

ed, the litter weight loss was lower than in the absence of the saprotroph. The suggested explanation for their results was that the mycorrhizal and saprotrophic fungi competed for available nutrients. With these nutrients sequestered by the mycorrhizal fungi, the saprotrophs were not able to immobilize nutrients to satisfy growth. The mycorrhizal hyphae, not being dependent on organic matter for their carbon supply, could outgrow the saprotrophs and fill all available hyphal niches.

In a repeat of their experiments by Berg and Lindberg[10] in Sweden, three alternative conclusions were drawn: 1) where root uptake of nutrients is excluded, more nutrients are available for microorganisms, thus there is a higher turnover of the saprotrophs and greater activity; 2) where root litter is removed, both easily metabolized carbon and nutrients in a readily mineralizable form are removed which could cause a lower microbial turnover; and 3) inhibiting substances could be involved. Inhibitors produced by the mycorrhizal fungi could reduce growth of the saprotrophs. These interactions in soil are, however, very complex and are an area for further research. However, as we shall see later, the possible outcome of competition between mycorrhizal and saprotrophic fungi to reduce rates of litter decomposition may not be at variance with the principle of mycorrhizal fungi possessing saprotrophic attributes.

Mycorrhizas and organic carbon decay

In 1948, Lindeberg[47] investigated the polyphenol oxidases of soil basidiomycetes. From his work he showed that few mycorrhizal fungi were able to produce these enzymes, although the production varied between species. Laiho[44] in his work on *Paxillus involutus* showed that his isolate of this fungus would not decompose cellulose or lignin in pure culture, although it was often found as the dominant fungus of decaying wood. Later work, however,[61,72,74] has shown that a wide variety of complex carbon sources can be degraded by a number of ectomycorrhizal fungal species. Although *Cenococcum geophilum*, *Amanita muscaria*, *Tricholoma aurantium*, *Rhizopogon luteolus*, and *R. roseus* were all shown to respire $^{14}CO_2$ from ^{14}C-labelled lignin and lignocellulose[74] the mycorrhizal fungi did so at a slower rate than the lignicolous fungi *Fomes annosus* and *Sporotrichum pulverulentum*.

Giltrap[29] screened 75 mycorrhizal fungi for their ability to produce polyphenol oxidase. Of these, only 18 produced significant quantities to degrade either gallic acid or tannic acid in agar culture. Only the four species of *Lactarius* (*rufus, tabidus, torminosus* and *uvidus*) could degrade both substrates. In a microcosm experiment of increasing levels of complexity, Dighton et al.[23] showed that *Pinus contorta* inoculated with the ectomycorrhizal fungi *Hebeloma crustuliniforme* and *Suillus luteus* could degrade hide powder, cotton and, to a lesser extent, chitin. In the case of both mycorrhizal fungi, however, the saprotrophic effect of the mycorrhizal fungus was suppressed on the addition of the basidiomycete decomposer fungus, *Mycena galopus*. There was also a highly significant effect of the presence of a plant root on the decomposition of the cotton and hide powder substrates, indicating that a root and mycorrhizal effect may be more important than the mycorrhizal fungus alone.

We have some evidence, therefore, to suggest that although deriving carbon from their host plant, some ectomycorrhizal fungi have the ability to produce enzymes to degrade complex carbohydrates either to gain carbon or the nutrient mineral elements they may contain.

Mycorrhizas and organic phosphorus

One of the most frequently studied nutrients whose uptake is influenced by mycorrhization of roots is phosphorus. Many studies have shown that mycorrhizal plants have higher total phosphate (concentration × biomass) and also higher phosphate concentration than non-mycorrhizal plants. Phosphorus is present in soil in three main forms: it may be in solution as orthophosphate, ionically bound in complex inorganic forms such as apatite, or covalently bound in organic complexes such as inositol hexaphosphates. In order for plants to access the organic forms of phosphates there is a need for the production of phosphatase or phytase enzymes. Saxena[64] demonstrated that roots of pea, grain, barley and wheat possessed phosphatase activity in the presence of sodium phytate as the phosphate source. He demonstrated that the phosphatase activity declined with increasing substrate concentration and, by comparing en-

zyme production between sterile plants and plants grown in non-sterile soil, indicated the importance of rhizosphere microflora in the production of enzymes.

The role of VA mycorrhizas in phosphate nutrition was demonstrated by Murdoch et al.[60] for maize, showing that mycorrhizal and non-mycorrhizal plants grew equally well on readily available phosphorus sources (rock phosphorus and superphosphate) but that the mycorrhizal plants grew better on less soluble sources (monocalcium and tricalcium phosphate).

In addition, the ability of VA mycorrhizas to produce extracellular or wall-bound phosphatases has been shown by a number of authors[7,8,24,25,40,52,81]. These authors have shown that production of phosphatase is suppressed by increasing orthophosphate concentrations in the growing medium and by increased phosphate concentrations in roots. As mentioned earlier in this paper, VA mycorrhizal-dominated communities tend to be associated with soils of low organic matter content and relatively high nutrient availabilities. The role of phosphatases in these fungi is unclear since access to poorly soluble inorganic forms of phosphorus does not depend on enzymes. In contrast, in organic soils where ericaceous and ectomycorrhizal fungi become dominant it would be advantageous to produce enzymes to degrade organic phosphate complexes, such as inositol hexaphosphate, which constitutes up to 40% of the total organic P in soil[4]. Indeed, these forms of phosphate have been shown to be as readily accessible to mycorrhizal endophytes of the ericaceous plants *Vaccinium macrocarpum, Rhododendron ponticum* and *Calluna vulgaris* as inorganic phosphates[57,66]. Similarly, phosphatase production by ectomycorrhizal fungi in pure culture has been demonstrated by a number of authors[6,11–13,16,17,33,36,39,41,58,59,69,70].

In the ectomycorrhizal fungi, phosphatase activity is induced in response to a lack of inorganic phosphate[3,11,13,16,39,58,59]. The amount of phosphatase or phytase activity varied between mycorrhizal species and between isolates of the same species. The activity was also equivalent to, or greater than, that of saprotrophic basidiomycetes[12,17]. By determination of the inorganic phosphate released into solution by the activity of pure cultures of ectomycorrhizal fungi, it was concluded that more inorganic phosphate was produced than required for fungal growth, indicating a source of phosphorus for the host plant[17,69] (table 2). Acid phosphatase production was also readily measured at low temperature (1 °C for *Hebeloma pusillum* and *Entoloma sericeum*)[6]. Activity at this temperature is advantageous for stressed environments such as the Arctic, where the optimal window for plant growth is limited by temperature and day length[49].

In addition to the demonstration of phosphatase and phytase production by mycorrhizal fungi in culture, enzyme activity has been noted from the surface of excised mycorrhizal roots[3,5,9,80]. Although roots for these studies were washed, there is always the possibility that rhizosphere microorganisms are also involved in the production of these enzymes and that they might work synergistically with the mycorrhizas. For example, Haussling and Marschner[31] showed greater phosphatase activity in rhizoplane soil compared with bulk soil and synergistic interactions between rhizospheric bacteria and mycorrhiza in host plant growth and phosphate nutrition have been demonstrated[42,43,46]. Further, direct evidence for utilization of organic phosphorus sources by mycorrhizas comes from radiotracer studies by Mejstrik and Krause[55] and Herrera et al.[34]. Although the work of Herrera's group was non-quantitative, they demonstrated, by autoradiography, uptake of ^{32}P-labelled phosphate into fungal and root material from labelled leaves. Mejstrik and Krause[55] used labelled humic organic phosphate (^{32}P immobilized in fungi and bacteria) and showed that *Cenococcum geophilum* and *Suillus luteus* mycorrhizal roots took up twice and four times as much label, respectively, as non-mycorrhizal roots. Conversely, however, Thomas and co-workers[71] using radiotracers, could not detect decomposition of complex or organic phosphate forms by *Thelephora terrestris* associated with Sitka spruce. Two explanations may exist: either the label in the earlier studies remained in an inorganic form and did not form organic complexes in the plant materials presented as resources for the mycorrhizas, or in the latter study, *Thelephora*, which is a nursery fungus ('r'-strategist) has not the enzymatic abilities to decompose organic phosphates.

Despite the overwhelming evidence for phosphatase production potential by ectomycorrhizal fungi in culture, there is a need to explore the activity of these enzymes in intact mycorrhizas and to look for their production not only at the root surface but in the distal hyphae at the site of resource capture.

Table 2. Inorganic phosphorus released into the growth medium as a percentage of the total inorganic phosphorus released from different forms of phytate by mycorrhizal and saprotrophic* fungi. Source of reference is given in parentheses.

	Form of phytate			
Fungus	Ca	Na	Fe	
Rhizopogon luteolus	52	70	77	(69)
Boletus granulatus	–	82	76	
Boletus (Suillus) luteus	70	85	80	
Cenococcum geophilum	72	88	30	
Paxillus involutus		83		(17)
Lactarius rufus		91		
Suillus luteus		7		
*Mycena galopus**		23		
*Marasmius androsaceous**		66		

Mycorrhizas and organic nitrogen

In the same way that phosphorus may be accessed from complex organic forms by mycorrhizas, it is now becoming apparent that nitrogen may also be derived from organic sources. This was first demonstrated by the studies of Lundeberg[50] who showed differences between ec-

tomycorrhizal fungal species to grow on a variety of nitrogen sources in culture. Ericaceous mycorrhizas have been shown to decompose a range of carbohydrate and organic nitrogen sources [62, 67] where growth of the endophyte on alanine and glutamic acid was equal to that on ammonium dihydrogen orthophosphate and higher than on ammonium or potassium nitrate. Endophytes failed to grow on humic and fulvic acids, however, although the saprotroph *Marasmius oreades* did.

Ectomycorrhizal fungi, such as *Suillus bovinus, Amanita muscaria, Paxillus involutus, Cenococcum geophilum* and *Rhizopogon roseolus* have been shown to use peptides and proteins as nitrogen sources in both pure culture of the fungus and in association with *Pinus contorta* [1, 2].

General discussion

We have seen above that there is a considerable body of evidence to show that mycorrhizas are capable of producing enzymes to allow them to derive mineral nutrients and carbon from organic resources. This facility has mainly been found in ectomycorrhizas and ericaceous mycorrhizas which are associated with soils of high organic matter content resulting from climatic limitations on rates of mineralization. The direct nutrient cycling system as envisaged by Went and Stark [79] and outlined in figure 2 would be of advantage to plants growing under such conditions. Similarly, in stressed environments, such as the Arctic tundra, where the window for biological activity, determined by temperature, water availability and light, is short, acquisition of nutrients directly from organic resources would be of benefit [49].

Within forest communities, conditions on the forest floor change with increasing age. The relative availability of nutrients from mineralization processes and demand by trees may not always be in balance. It has been demonstrated that demand outweighs availability at a time when maximum species diversity of ectomycorrhizal fungi occurs. It has been hypothesised [21, 45] that at this stage in forest development the mycorrhizal community may switch to the utilization of organic resources for the derivation of mineral nutrients. Some of the recorded incidences of enzyme production and organic substrate utilization in relation to mycorrhizal succession are given in table 3. Although table 3 shows a trend for increased enzymatic capabilities in fungal genera associated with late-stage mycorrhiza sensu Mason et al. [53, 54] it must be borne in mind that there is a great deal of variability within genus and within species, for example in isolates from different localities [82]. However, a number of important genera occurring in mid rotation forests *Inocybe, Cortinarius, Russula* are difficult to grow in axenic culture. It is, therefore, interesting to speculate about their role in the utilization of organic substrates as they obviously have specific requirements in artificial growth media which are not satisfied by the media commonly used to culture ectomycorrhizal fungi.

The work of Gadgil and Gadgil [27, 28] suggested that the presence of mycorrhizal roots suppressed litter decomposition. This, however, should not necessarily be taken to

Table 3. The generalized succession of different genera of mycorrhizal fungi with increasing forest stand (tree) age and their ability to degrade organic nutrient sources.

Dominant mycorrhizal fungal genera	Forest (tree) age Young ←				→ Old	References
	Thelephora	*Hebeloma* *Laccaria* *Rhizopogon* *Paxillus*	*Lactarius* *Cortinarius* *Leccinum* *Inocybe*	*Russula* *Amanita* *Boletus*[1] (*Laccaria*) *Suillus*[1]		22 ([1] General observations)
Enzyme (substrate)	Enzymatic capability Poor ←				→ Good	
Phosphatase	*Laccaria* *Suillus*		*Hebeloma* *Pisolithus*[2]		*Suillus*	58
Phosphatase	*Piloderma*	*Rhizopogon* *Thelephora*	*Amanita*		*Laccaria* *Hebeloma*	56
Phosphatase	*Hebeloma*				*Cenococcum*[2]	5
Phytase	*Suillus*	*Suillus*	*Pisolithus*	*Laccaria*	*Hebeloma* *Suillus*	58
(Gallic acid)	*Hebeloma* *Suillus* *Rhizopogon*	*Cenococcum*[2]	*Suillus*	*Leccinum*	*Lactarius* *Amanita*	29
(Tannic acid)	*Hebeloma*	*Leccinum* *Paxillus* *Rhizopogon*	*Boletus* *Suillus* *Cenococcum*[2]		*Lactarius*	29
(Protein)	*Laccaria*	*Lactarius*	*Paxillus* *Suillus*	*Rhizopogon* *Cenococcum*[2]	*Amanita*	2

[2] There is little information on the occurrence of *Cenococcum* in relation to forest development. *Pisolithus* is probably more common in early forest growth but, again, there is little information in the literature.

mean that mycorrhizal fungi are not capable of degrading organic materials in soil. If the mycorrhizal fungi suppress the activity of saprotrophic fungi by competition for physical space or by production of antagonistic by-products, they would then be able to have unrivalled access to a nutrient source which they could utilize at a rate commensurate to the sink strength of the host plant. This concept would fit into the theoretical considerations of succession, where 'K'-strategists become highly conservative as does the ecosystem itself[33].

The whole subject is far from completely understood. Most work to date has been carried out under laboratory conditions, often using the fungal symbiont in isolation from its host root. There is a need to demonstrate degradation of organic substrates in the field by mycorrhizas and to also look at the intact mycorrhizal system. Excised mycorrhizas have lost their extraradical hyphal connections to the substrate. Enzyme production by excised mycorrhizas cannot easily be separated into the root or fungal component. It is because of this that the intact system needs to be studied to evaluate the relative role of each component and to look at the physiology of the distal end of the hyphae where the relevant interaction between the fungus and the substrate occurs.

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