Chapter (non-refereed)

Mason, P. A.; Last, F. T.. 1986 Are the occurrences of sheathing mycorrhizal fungi in new and regenerating forests and woodlands in Scotland predictable? In: Jenkins, D., (ed.) *Trees and wildlife in the Scottish uplands.* NERC/ITE, 63-70. (ITE Symposium, 17).

Are the occurrences of sheathing mycorrhizal fungi in new and regenerating forests and woodlands in Scotland predictable?

P A MASON and F T LAST
Institute of Terrestrial Ecology, Edinburgh

1 Introduction

To many people, the names 'deceiver', 'brown rim roll' and 'blusher' may suggest varieties of butterflies, but in the event they, like 'poison pie', 'blewit', and 'fly agaric', refer to ground fungi that develop in woodlands and forests. Poison pie (*Hebeloma crustuliniforme*) is usually associated with young trees, while blewits (*Tricholoma* spp.) and fly agaric (*Amanita muscaria*) are linked with older trees. The bolete *Suillus luteus* is strongly associated with pines, while other fungi are less restricted in their choice of hosts. There is, therefore, evidence to suggest that toadstools within forests and woodlands do not occur at random. What are the 'rules' governing their occurrence? Are they the same in natural/semi-natural woodlands and man-made plantations? Are they the same in second rotations as in first rotations, remembering that soils in the former will have been ameliorated by the preceding stand. These are matters of interest in the Highlands of Scotland where afforested areas are likely to increase and where existing plantations will be felled and replanted.

It is now recognized that 'soil fungi' have an important role to play in the cycling of nutrients and energy in terrestrial ecosystems (Harley 1971). Many species of soil fungi are decomposers that can actively break down moribund tissues of both plants and animals, with the release of carbon dioxide and a variety of soluble compounds, many of which are absorbed by later generations of plants and animals in addition to other microbes. Plant litter, twigs, wood and/or roots are colonized by ordered sequences of saprotrophic fungi. These early colonizers, the primary decomposers, are being replaced by an array of secondary decomposers, including many basidiomycetes. This sequence of microbes with different capabilities ensures that even the lignin and cellulose components of plant material are degraded to soluble substances (Harley & Waid 1955; Harley 1971; Frankland 1981). Fungal successions would, therefore, seem to be commonplace within forest ecosystems.

In addition to decomposers, the reservoir of soil microbes includes many fungi that can colonize roots of trees and subsequently form mycorrhizas. Within the UK, trees in the Rosaceae (eg species of apple (*Malus*), cherry (*Prunus*) and pear (*Pyrus*)) and Aceraceae (sycamore (*Acer pseudoplatanus*)) develop, like most herbs and shrubs, vesicular–arbuscular (endo-)mycorrhizas with members of the Endogonaceae, whereas the majority of trees including pine (*Pinus* spp.), spruce (*Picea* spp.), larch (*Larix* spp.), fir (*Abies* spp.), willow (*Salix* spp.), lime (*Tilia* spp.), oak (*Quercus* spp.), beech (*Fagus* spp.) and birch (*Betula* spp.) develop sheathing (ecto-)mycorrhizas with an array of mostly basidiomycetous and ascomycetous fungi. Interestingly, the genera of mycorrhizal fungi listed for Scotland (Table 1) are similar to those recorded for high-altitude locations in southern India (Last & Fleming 1985).

Table 1. Genera of fungi that have been recorded in woodlands and forests in Scotland (source: Watling 1984a,b)

Agaricus	**Gomphidius*	*Oudemansiella*
**Amanita*	**Hebeloma*	**Paxillus*
**Amphinema*	*Hygrophorus*	*Peziza*
**Boletus*	*Hypholoma*	*Pholiota*
**Cantharellus*	**Inocybe*	*Psathyrella*
**Cenococcum*	**Laccaria*	**Rhizopogon*
Clitocybe	**Lactarius*	**Russula*
Collybia	**Leccinum*	**Scleroderma*
**Chroogomonophus*	*Lepiota*	**Suillus*
**Cortinarius*	*Lepista*	**Thelephora*
Cystoderma	*Marasmius*	**Tomentella*
**Elaphomyces*	*Mycena*	**Tricholoma*
Entoloma	**Naucoria*	**Tuber*
Galerina	*Nolanea*	

*Genera with species proven or suspected of being able to form sheathing mycorrhizas with roots of trees

Mycorrhizas facilitate the uptake of nutrients which may otherwise remain unavailable to their hosts; they can also produce growth stimulatory substances which may enhance the growth and longevity of roots (Slankis 1973). In return, mycorrhizal fungi, to a greater or lesser extent, depend on their hosts for supplies of energy. If they are deprived of access to their hosts' current assimilates, either by root severance or defoliation, sheathing mycorrhizal fungi appear unable to produce fruitbodies (Last *et al.* 1979). Although sheathing mycorrhizas seem essential for sustained growth in forests, surprisingly little is known about the factors controlling their occurrence. Do they, like decomposers, occur in ordered sequences? Bearing in mind the changes that occur among non-parasitic microbes which colonize living leaves and roots, it would, by analogy, be surprising if the fungi forming sheathing mycorrhizas with trees 40 years old were the same as those colonizing the roots of saplings. If there are differences, can they be explained and predicted, and how should they influence our approach to the future management of forests in the Highlands?

2 Occurrence of mycorrhizal fungi in 'primary' woodlands and forests

Mycorrhizal fungi which develop in stands of trees growing on sites that have been treeless for many years ('primary' woodlands) are likely to be substantially different from those in 'secondary' woodlands where seedlings grow either among mature trees or on sites where mature trees have only recently been clearfelled.

2.1 From establishment to canopy closure

Trappe (1962, 1977) estimated that more than 2000 species of fungi have the potential to form mycorrhizas. Most of these fungi form readily identifiable fruitbodies, including toadstools, earth balls, earth fans and elf cups, which have formed the focus of attention of innumerable fungal forays. While recording the presence of these often colourful fungi, however, mycologists have rarely added detailed habitat data such as the state of woodland development (before or after canopy closure), or the soil type.

While it has long been recognized that species of birch (*Betula*), major components of the Scottish countryside, are able to invade open ground and colonize gaps within established woodlands (Kirby 1984), it is only during the last few years that it has become clear that the fungi forming sheathing mycorrhizas on pioneer sapling birch are likely to differ from those associated with mature birch. By studying the sequence of fruitbodies associated with silver birch (*Betula pendula*) and downy birch (*B. pubescens*) during the first 10 years after outplanting at the Bush Estate, Midlothian (lat. 55°52'N), Mason *et al.* (1982, 1983) identified an ordered array, in time and space, of mycorrhizal fungi. During the second to fourth year after planting, they recorded species of *Hebeloma, Inocybe, Laccaria* and *Thelephora*, which are not usually associated with mature birches: in years 6–10, fruitbodies of species of *Cortinarius, Leccinum* and *Russula* appeared (Table 2). Paralleling these changes in types of fungi, there were also changes in numbers of different species associated, at any one time, with ageing trees. Numbers increased from 4 per tree in year 3 to nearly 30 in year 10 (Last *et al.* 1983), with a consistently greater variety of fungi associated with silver birch than with downy birch (Mason *et al.* 1982).

The fruitbodies of fungi associated with 3-year-old lodgepole pine (*Pinus contorta*), growing in the same field as the birches already mentioned, included *Rhizopogon luteolus, Suillus luteus* and *Amphinema byssoides,* in addition to species of *Hebeloma* (*H. fragilipes*) and *Thelephora* (*T. terrestris*) (J H Warcup pers. comm.). Species of *Hebeloma* are thought to be pioneer fungi colonizing the roots of young saplings (eg *Hebeloma fragilipes* with pine, *H. populinum* with Sitka spruce (*Picea sitchensis*), and *H. versipelle* with lime (*Tilia cordata*) (Watling 1981)).

The fruitbodies associated with stands of lodgepole pine and Sitka spruce, growing in peat in Northumberland, changed from *Laccaria* spp. and *Paxillus involutus* when trees were 3–4 years old to species of *Inocybe, Lactarius, Cortinarius* and *Russula* when the trees were older (Dighton *et al.* 1986). Although Dighton's study did not detail the first appearance of each fungus, the available evidence suggests that *Laccaria* was followed by *Lactarius rufus*, to be joined, in turn, by *Inocybe longicystis, Cortinarius croceofolius* and *Russula emetica* before canopy closure. A nearly identical sequence was observed in conjunction with stands of Sitka spruce, namely *Laccaria* spp. → *Inocybe longicystis* → *Lactarius rufus* → *Cortinarius croceofolius.*

From the occurrence of fruitbodies, it is apparent that similar sequences of mycorrhizal fungi were associated with lodgepole pine and Sitka spruce in peaty soils in northern Britain. The differences between these sequences were less than those between 2 stands of the same species (lodgepole pine) growing at different locations (*vide* Dighton and Warcup). It, therefore, seems that fungi occurring early in mycorrhizal successions are not host-specific. Furthermore, lodgepole pine, at different locations, can associate with a variety of early-stage mycorrhizal fungi. This capability probably helps the establishment of pioneer trees in a variety of habitats. Kropp and Trappe (1982)

Table 2. Succession of fruitbodies of proven or suspected sheathing mycorrhizal fungi appearing in a stand of birches planted at Bush Estate, near Edinburgh (source: Last *et al.* 1983)

Years after planting	Fungi whose fruitbodies occurred for the first time
1	Nil
2	*Hebeloma crustuliniforme* (Bull. : St. Amans) Quelet
	Laccaria proxima (Boud.) Pat.
3	*Laccaria tortilis* ({Bolt.} S. F. Gray) Cooke
	Thelephora terrestris Ehrenb. : Fr.
4	*Hebeloma fragilipes* Romagnesi
	H. sacchariolens Quelet
	H. mesophaeum (Pers. : Fr.) Quelet
	Inocybe lanuginella (Schroet.) Konrad and Maublanc
	Lactarius pubescens (Fr. : Krombh.) Fr.
6	*Cortinarius* sp.
	Hebeloma leucosarx P. D. Orton
	Hymenogaster tener Berkeley and Broom
	Inocybe petiginosa (Fr. : Fr.) Gillet
	Leccinum roseofracta Watling
	L. scabrum (Bull. : Fr.) S. F. Gray
	L. versipelle (Fries and Hök) Snell
	Peziza badia Persoon ex Merat
	Ramaria sp.
7	Other *Cortinarius* spp.
	Other *Hebeloma* spp.
	Lactarius glyciosmus (Fr. : Fr.) Fr.
	Leccinum subleucophaeum Dick and Snell
10	*Hebeloma vaccinum* Romagnesi
	Russula betularum Hora
	R. grisea (Pers. : Secr.) Fr.
	R. versicolor J. Schaeff
14	*Laccaria laccata* (Scop. : Fr.) Cooke
	Lactarius spinosulus Quelet
	Russula atropurpurea (Krombh.) Britz.

also noted that western hemlock (*Tsuga heterophylla*), which in nature grows in mixed stands, usually associates with mycorrhizal fungi that are not host-specific. In contrast, 'early' fungi associated with red alder (*Alnus rubra*) tend to be host-specific, so possibly helping to explain why this tree grows in pure stands.

Sequences of mycorrhizal fungi similar to those occurring in the northern hemisphere have been found in association with young conifers growing in New Zealand (Chu-Chou 1979; Chu-Chou & Grace 1981). As with young stands of lodgepole pine in Scotland, species of *Hebeloma* and *Rhizopogon* were found in association with Monterey pine (*Pinus radiata*) growing in New Zealand (Chu-Chou 1979). *Hebeloma crustuliniforme* was soon replaced by *Laccaria* spp. and 2 species of *Inocybe* and *Suillus*. Taken together, these observations in temperate regions of the world suggest that some mycorrhizal fungi (eg *Hebeloma, Laccaria, Inocybe* and *Thelephora*) are characteristic of young stands of trees growing at 'primary' sites.

Support for the concept of mycorrhizal succession in birch has been provided by J H Warcup (pers. comm.) and Deacon *et al.* (1983) at Bush Estate. They found that the above-ground fruitbodies were associated with their own distinctive types of below-ground mycorrhizas (Plate 10). Additional evidence, however, indicates that the range of early-stage fungi forming mycorrhizas on young trees can be modified by soil type and genotypic differences within species of trees (Last *et al.* 1984). While all seedlings within a seed lot would associate with early-stage fungi, one might be linked with *Hebeloma* spp., whereas another might form mycorrhizas with *Inocybe* spp. The effects of soil type were highlighted in inoculation experiments with *Hebeloma sacchariolens* (Last *et al.* 1985). While *H. sacchariolens* continued to dominate root systems of inoculated birch seedlings when growing in mineral soils and sedge peat, it was completely replaced by naturally occurring fungi in a more acidic *Sphagnum* peat. In the USA, there is a suggestion of a broader environmental effect. While the mycorrhizal fungus *Pisolithus tinctorius* facilitated the establishment of pine seedlings in south-eastern USA (Marx 1980), it seems to have been of little value in cooler more northerly areas (Grossnickle & Reid 1983), where species of *Laccaria* appear to be more successful (Molina & Trappe 1982).

2.2 From canopy closure to maturity

As the canopies of trees begin to overlap, forest environments change, with temperatures and moisture conditions at ground level becoming less favourable for litter breakdown and nutrient mobilization by saprotrophic fungi (Swift *et al.* 1979; Vogt *et al.* 1983a).

With changes in the activities of saprotrophic fungi, it would be logical to expect corresponding changes in the activities of mycorrhizal species. After canopy closure, Vogt *et al.* (1983b) recorded that the biomasses of mycorrhizal fungi (which were not identified) associated with conifers in nutrient-poor sites were significantly larger than those associated with conifers at nutrient-rich sites. In contrast, instead of measuring fungal biomass, Watling (1984a) has concentrated on the identification of woodland macrofungi. After repeatedly visiting 19 woodland sites near the Kindrogan Field Centre, Perthshire, he established that 27% of the 540 recorded species of agarics were attributable to 4 genera of mycorrhizal fungi (*Cortinarius* (45 species), *Lactarius* (38 species), *Russula* (57 species) and *Amanita* (7 species)).

More recently, Dighton *et al.* (1986), who counted numbers of fruitbodies, found that the diversity of mycorrhizal fungi in stands of lodgepole pine decreased after canopy closure, and *Russula emetica* became dominant. This decrease in diversity in stands of mature conifers parallels the observations of Harvey *et al.* (1976), who indicated that root systems of Douglas fir (*Pseudotsuga menziesii*) and western larch (*Larix occidentalis*) were dominated by *Russula brevipes* and *Suillus cavipes* respectively. Richardson (1970), like Dighton, found that populations of toadstools attributable to mycorrhizal fungi in a mature (55-year-old) plantation of Scots pine (*Pinus sylvestris*) were dominated by *Russula emetica,* but with significant numbers of *Amanita* (*A. inaurata, A. rubescens, A. vaginata*) and *Lactarius* (*L. rufus, L. turpis*).

These observations show that the mycorrhizal fungi occurring in Scottish birchwoods are similar to those found in Scandinavia (Watling 1984b), to the extent that the 2 colour 'forms' of *Lactarius vietus* in Scotland have their counterparts in Scandinavia. Of the small group of *Amanita* species found in European birchwoods, *A. muscaria* is the best known. It has been recorded in the northern and southern hemispheres in association with mature stands of several tree species, although in southern India it appears in association with much younger trees, possibly because forests develop canopies more rapidly there than in temperate areas (Last *et al.* 1981). *Amanita crocea,* in contrast to *A. muscaria,* is usually found in troops (groups) in Scottish birchwoods (Watling 1984b). Species of *Russula* and *Lactarius* are also common in birchwoods, excepting *R. aquosa* (which has only recently been added to the British list) and the rare agaric *R. scotica* which is confined to Scotland (Watling 1984b).

Together, the data indicate that mature woodlands and forests in Scotland have mycorrhizal floras distinct from those associated with young stands of trees. Mature woods are characterized by species of *Amanita, Cortinarius, Lactarius, Russula* and *Tricholoma*. There is, however, a suggestion that the diversity of mycorrhizal fungi peaks at, or about, the time of canopy closure. Nevertheless, knowledge of the temporal changes occurring after canopy closure is at

present fragmentary. Miles (1985), when observing stands of silver birch of different ages at Kerrow, Inverness-shire, found that most fruitbodies in a stand 20 years old were attributable to *Cortinarius* spp. and *Lactarius pubescens,* whereas in a stand 72 years old fruitbodies of *Amanita muscaria, Tricholoma columbetta, Laccaria amethystea* and *Lactarius tabidus* were the most numerous.

3 Occurrence of mycorrhizal fungi in 'secondary' woodlands and forests

Our knowledge of the ecology of mycorrhizal fungi in 'primary' woodlands and forests has steadily increased, but what happens when clearfelled areas are replanted or when seedlings regenerate naturally within established woodlands?

3.1 Naturally regenerating woodlands

Present evidence, although scant, suggests that mycorrhizal sequences on seedlings regenerating naturally within natural woodlands or forests may differ from those on seedlings establishing at 'primary' sites. Although soils within natural woodlands throughout Great Britain are likely to possess spores of wind-dispersed early-stage fungi, most roots of regenerating tree seedlings seem to be colonized by late-stage fungi. For example, 73% of a naturally occurring population of birch seedlings growing in a sweet chestnut (*Castanea sativa*) coppice in southern England were found at the end of the first year to have mycorrhizas attributable to late-stage boletes (Fleming 1983). In an attempt to explain this 'anomaly', Fleming planted birch seedlings (which had been propagated in sterile (axenic) conditions and were therefore without mycorrhizas) among the roots of ageing birch trees (Fleming 1983; Fleming *et al.* 1986). In one instance, the roots of the mature trees were left undisturbed, while in another they were severed by coring and trenching.

These treatments were tested at 2 sites: Bush Estate, with a stand of birch newly developing on former agricultural land, and Struan Wood, Perthshire, with a long-established mature birchwood. Irrespective of site, seedlings planted among undisturbed roots developed late-stage mycorrhizas. However, where they were planted among severed roots, there was a strong site effect. At Bush, most of the mycorrhizas that developed on the experimental seedlings were attributable to early-stage fungi, whereas at Struan many mycorrhizas were formed by species of the late-stage *Lactarius* and *Leccinum.*

Severing roots and depriving inocula (strands) of *Lactarius* and *Leccinum* of their sources of host assimilates prevented them from forming mycorrhizas on seedlings planted at Bush but not at Struan. The ability of late-stage fungi to outcompete early-stage fungi in naturally regenerating woodlands seems to reflect their ability to form strands and/or their responses to changing soil conditions, the most important aspect of which may be the accumulations of organic matter which occurred at Struan but not at Bush.

3.2 Second rotation plantations

Compared with naturally regenerating woodlands, even less is known of the fungi which colonize seedlings on sites being afforested for a second time. For how long does the inoculum (largely of late-stage fungi) present on roots of clearfelled stumps remain viable and able to colonize roots of seedlings, in the absence of currently produced host assimilates? How long does this capability persist, compared with the viability of propagules, probably mostly spores of early-stage fungi? Should the fate of cut stumps, and their associated mycorrhizas, be a consideration when planning the preparation of sites for second rotations? The answers will, of course, depend upon the early- or late-stage fungi which seem most appropriate for second and subsequent rotations. First, however, it is necessary to ascertain the sequence of mycorrhizal fungi, and their roles, on young seedlings planted at second rotation sites.

4 Factors influencing mycorrhizal distribution

Early- and late-stage mycorrhizal fungi seem able to form mycorrhizas with equal facility in sterile, axenic conditions (Mason 1980). However, results of controlled inoculation experiments indicate that late-stage fungi, unlike early-stage fungi, are unable to form mycorrhizas, because of their lack of competitiveness, on seedlings growing in first rotation unsterile forest soils (Table 3). In corroboration, laboratory experi-

Table 3. Factors possibly influencing the sequence of fungi forming sheathing mycorrhizas with tree roots (source: Dighton & Mason 1985)

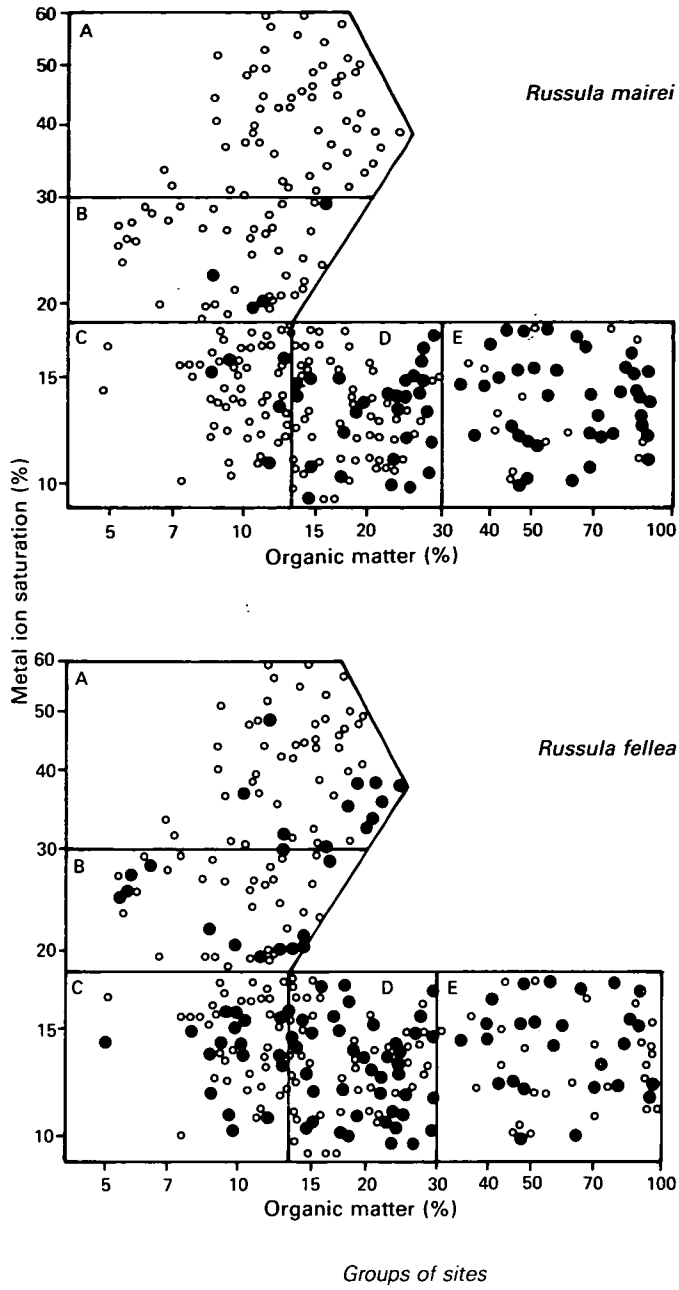
Factors affecting the ability of mycorrhizal fungi to colonize roots	Occurrences of different fungi in mycorrhizal succession*	
	Early	Late
Energy demand (as judged by growth on artificial media)	Small	Large
Conjectured ability to supply nutrients to trees	Capable of supplying hosts with nutrients from labile inorganic pool	Capable of supplying hosts with nutrients from labile inorganic pool also, because of the possession of appropriate extracellular enzymes, from the organic pool
Competitive ability:		
Ability of fungi to form mycorrhizas on tree seedlings growing in first rotation soils which were		
i. partly sterilized	+	+
ii. untreated (not partially sterilized)	+	–

*Mycorrhizal succession *sensu* Mason *et al.* 1982; Deacon *et al.* 1983; Last *et al.* 1983

ments with artificial substrates showed that early-stage fungi are less glucose-demanding than late-stage fungi (Dighton & Mason 1985). It has also been suggested that early-stage mycorrhizal fungi are better suited to the colonization of seedlings growing in mineral soils than in organic soils (Alvarez *et al.* 1979), whereas late-stage mycorrhizal fungi prefer organic substrates (Harvey *et al.* 1976). On a mining site, Gardner and Malajczuk (1985) found that the early-stage fungus *Laccaria* fruited on the unaltered ridges, whereas the late-stage *Cortinarius* fruited in the litter-filled troughs associated with the planting of 5 species of eucalypts (*Eucalyptus* spp.).

However, because early-stage *Laccaria* spp. are able to colonize seedlings growing in peat, an organic substrate (Last *et al.* 1985), the suggestions made by Alvarez *et al.* (1979) and Harvey *et al.* (1976) need qualification. Accepting that the effects of organic matter on the formation of mycorrhizas and the production of fruitbodies may differ, it seems that late-stage fungi can colonize roots in soils which have been amended by plant litter, but not in soils, mineral and organic, which have not been altered in this way. Tyler (1984) found that the production of fruitbodies in beech woodlands by the late-stage *Russula mairei* and *R. fellea* was directly related to amounts of organic matter in surface soils (Figure 1).

The ability of late-stage fungi, in preference to early-stage fungi, to colonize and form mycorrhizas on seedlings growing in soils modified by the deposition and subsequent decomposition of litter may be a reflection of the ability of the fungi to produce extracellular enzymes. This characteristic might be particularly important because soil environment changes occurring at, or after, canopy closure seem likely to restrict litter decomposition and mobilization by other soil microbes (Vogt *et al.* 1983a). Bartlett and Lewis (1973) detected phosphatase and phytase in mycorrhizal roots collected from mature beech trees, whereas Giltrap (1982) found that a number of mycorrhizal fungi were able to produce polyphenol-oxidases, and Linkins and Antibus (1981) detected appreciable cellulase activity in the mycorrhizal roots of 'least' willow (*Salix rotundifolia*). Interestingly, exocellulase and β-glucosidase activities were 60 and 140 times greater in soil-permeating hyphal strands of mycorrhizal fungi than in the mantles of their mycorrhizas. Much remains to be learnt. The mechanisms controlling mycorrhizal development in 'primary' and 'secondary' woodlands need to be clarified so as to ensure that the correct fungi are inoculated to saplings being planted in 'primary' and 'secondary' sites.



	Groups of sites				
	A	*B*	*C*	*D*	*E*
Soil characteristics					
Metal ion saturation (%)	<60–30	<30–18	<18	<18	<18
Organic matter (%)	13	<13	<13	13–30	>30–93
Occurrence (%) of fruitbodies attributable to					
Russula mairei	Nil	8	9	32	72
R. fellea	19	27	35	45	53

Figure 1. Autumn occurrence (%) of fruitbodies of 2 mycorrhizal fungi, Russula mairei *and* R. fellea, *found in association with stands of beech growing at a range of sites with different soils in southern Sweden. Soil data refer to top 5 cm after removing superficial litter (•, sites with fruitbodies; ○, sites without fruitbodies) (source: Tyler 1984).*

5 Conclusions

During the development of 'natural' and man-made forests, soil properties change, especially in the surface horizons where mycorrhizas are active. It is therefore not surprising that observations of the production of fruitbodies and the occurrence of myco-

rrhizas have lent support to the concept of mycorrhizal succession. While these changes seem clear-cut in 'primary' woodlands in Scotland and other temperate areas, the data, as yet fragmentary, suggest that mycorrhizal development in 'secondary' woodlands is restricted to late-stage fungi.

The mechanisms controlling mycorrhizal development are far from obvious, although it is already apparent that several factors are involved. Possibly because they need few carbohydrates for rapid growth, early-stage fungi initially outcompete late-stage fungi when trees colonize or are planted on sites which were previously unafforested. However, with the accumulation, decomposition and incorporation of litter into the upper soil horizons, the conjectured ability of late-stage fungi, with the help of exoenzymes, to derive augmented sources of energy from the organic matter enriching the surface horizons seems to swing the balance in favour of late-stage fungi. This advantage could be magnified by the formation of mycelial strands which many late-stage fungi are able to form.

After becoming established in 'primary' woodlands, late-stage mycorrhizal fungi thereafter seem to hold sway, unless soil properties change in intervals between successive stands of trees and/or if the propagules (strands/spores) of late-stage fungi lose viability sooner than those of early-stage fungi. Interestingly, Read *et al.* (1985) have indicated that strands of mycorrhizas may transfer carbohydrates from mature trees to seedlings, thus giving tree seedlings in dense forests an advantage when they attempt to maintain themselves in suboptimal light conditions. This may be a good reason for using late-stage fungi in managing secondary woodlands.

These ideas now need to be examined experimentally, recognizing that they may help elucidate (i) the balance of factors determining the survival and fruitbody production of different fungi, and (ii) the benefits that may accrue to their 'tree' hosts. At the same time, they may guide the rational choices of mycorrhizal fungi for the controlled inoculation of saplings to be planted in 'primary' and 'secondary' sites. The choices may differ.

At the present time, no discussion of the dynamics of forests in western Europe can be complete without reference to the possible influences of atmospheric pollutants, regrettably encompassed by the umbrella term 'acid rain'. Recently, as a result of monitoring the occurrence of fruitbodies at intervals since 1912, colleagues have inferred that the production of toadstools by many agarics has appreciably decreased in the Netherlands, the decreases being particularly notable among mycorrhizal fungi in woodlands at acidic, sandy sites (Arnolds 1985). However, are events in sandy soils mirrored by those in other, equally acid, types of soil? Are inverse associations with atmospheric pollutants indicators of causal relationships? Are there other plausible explanations of the decreases? Even if the production of fruitbodies has decreased, have the ameliorating effects of mycorrhizal fungi on tree growth been adversely affected? Whatever the answers to these questions, it is perhaps appropriate to develop a more rational and objective approach to the conservation of fungi. They play a vital role in the cycling of nutrients, both as 'decomposers' and, as discussed in this paper, in facilitating the uptake and movement of nutrients through mycorrhizal associations.

6 Summary

Many fungi produce fruitbodies in forests and woodlands. Some are plant pathogens, while others either decompose moribund tissues or form sheathing (ecto-)mycorrhizas.

Gradually accumulating evidence suggests that sheathing mycorrhizal fungi associated with tree seedlings on new, primary, sites differ from those colonizing seedlings regenerating within mature woods or planted into secondary areas that have recently been clearfelled.

In the former, many of the sheathing mycorrhizas are attributable to species of *Hebeloma, Laccaria* and *Inocybe* (early-stage fungi), whereas in the latter they may be formed by species of *Amanita, Cortinarius, Lactarius, Russula* and *Tricholoma,* a fungal group found to be associated with ageing trees on primary sites where they have been designated late-stage fungi.

Why are seedlings in primary sites colonized by early-stage mycorrhizal fungi, whereas those in secondary sites seem to associate with late-stage fungi? The answer to this question is needed to ensure that seedlings planted into primary and secondary sites, which are abundant in the uplands, are inoculated with the appropriate fungi if and when controlled inoculations, during or immediately after propagation, are adopted. To date, evidence suggests that late-stage fungi are unable to compete in newly established primary woodlands. In contrast, they are able to monopolize roots (whether of ageing trees in 'primary' woods or of seedlings in 'secondary' loccations) growing in soils which were modified during earlier tree growth, possibly by the incorporation of decomposing litter. It is suggested that the production of pectolytic and cellulytic enzymes by late-stage fungi may favour them in modified soils at the expense of early-stage fungi.

7 References

Alvarez, I.F., Rowney, D.L. & Cobb, F.W. Jr. 1979. Mycorrhizae and growth of white fir seedlings in mineral soil with and without organic layers in a California forest. *Can. J. For. Res.*, **9,** 311–315.

Arnolds, E., ed. 1985. Veranderingen in de paddestoel–flora (mycoflora). *Wet. Meded. K. ned. natuurh. Veren.*, no. 167.

Bartlett, E.M. & Lewis, D.H. 1973. Surface phosphatase activity of mycorrhizal roots of birch. *Soil Biol. Biochem.*, **5,** 249–257.

Chu-Chou, M. 1979. Mycorrhizal fungi of *Pinus radiata* in New Zealand. *Soil Biol. Biochem.*, **11,** 557–562.

Chu-Chou, M. & Grace, L.J. 1981. Mycorrhizal fungi of *Pseudotsuga menziesii* in the north island of New Zealand. *Soil Biol. Biochem.*, **13,** 247–249.

Deacon, J.W., Donaldson, S.J. & Last, F.T. 1983. Sequences and interactions of mycorrhizal fungi on birch. *Pl. Soil,* **71,** 257–262.

Dighton, J. & Mason, P.A. 1985. Mycorrhizal dynamics during forest tree development. In: *Developmental biology of higher fungi,* edited by D. Moore, L.A. Casselton, D.A. Wood & J.C. Frankland, 117–139. Cambridge: Cambridge University Press.

Dighton, J., Poskitt, J.M. & Howard, D.M. 1986. Changes in occurrence of basidiomycete fruitbodies during forest stand development: with specific reference to mycorrhizal species. *Trans. Br. mycol. Soc.* In press.

Fleming, L.V. 1983. Succession of mycorrhizal fungi on birch: infection of seedlings planted around mature trees. *Pl. Soil,* **71,** 263–267.

Fleming, L.V., Deacon, J.W. & Last. F.T. 1986. Ectomycorrhizal succession in a Scottish birch wood. *Proc. European Symposium on Mycorrhizae, 1st.* Dijon: Institut National de Recherches Agronomiques. In press.

Frankland, J.C. 1981. Mechanisms in fungal successions. In: *The fungal community: its organisation and role in the ecosystem,* edited by D.T. Wicklow & G.C. Carroll, 403–426. New York: Marcel Dekker.

Gardner, J.N. & Malajczuk, N. 1985. Succession of ectomycorrhizal fungi associated with eucalypts on rehabilitated bauxite mines in South Western Australia. In: *Proc. N. American Conference Mycorrhizae, 6th,* edited by R. Molina, 265. Corvallis, OR: Oregon State University Press.

Giltrap, N.J. 1982. Production of polyphenol oxidases by ectomycorrhizal fungi with special reference to *Lactarius* spp. *Trans. Br. mycol. Soc.*, **78,** 75–81.

Grossnickle, S.C. & Reid, C.P.P. 1983. Ectomycorrhiza formation and root development of conifer seedlings on a high-elevation mine site. *Can. J. For. Res.*, **13,** 1145–1158.

Harley, J.L. 1971. Fungi in ecosystems. *J. Ecol.*, **59,** 653–668.

Harley, J.L. & Waid, J.S. 1955. A method of studying active mycelia on living roots and other surfaces in the soil. *Trans. Br. mycol. Soc.*, **38,** 104–118.

Harvey, A.E., Larsen, M.J. & Jurgensen, M.F. 1976. Distribution of ectomycorrhizae in a mature Douglas fir-larch forest soil in western Montana. *Forest Sci.*, **22,** 393–398.

Kirby, K.J. 1984. Scottish birchwoods and their conservation - a review. *Trans. bot. Soc. Edinb.*, **44,** 205–218.

Kropp, B.R. & Trappe, J.M. 1982. Ectomycorrhizal fungi of *Tsuga heterophylla. Mycologia,* **74,** 479–488.

Last, F.T. & Fleming, L.V. 1985. Factors affecting the occurrence of fruitbodies of fungi forming sheathing (ecto-) mycorrhizas with roots of trees. *Proc. Indian Acad. Sci. (Plant Sci.),* **94,** 111–127.

Last, F.T., Pelham, J., Mason, P.A. & Ingleby, K. 1979. Influence of leaves on sporophore production by fungi forming sheathing mycorrhizas with *Betula* spp. *Nature, Lond.*, **280,** 168–169.

Last, F.T., Mason, P.A., Smith, R.I., Pelham, J., Bhoja Shetty, K.A. & Mahmood Hussain, A.M. 1981. Factors affecting the production of fruitbodies of *Amanita muscaria* in plantations of *Pinus patula. Proc. Indian Acad. Sci. (Plant Sci.),* **90,** 91–98.

Last, F.T., Mason, P.A., Wilson, J. & Deacon, J.W. 1983. Fine roots and sheathing mycorrhizas: their form, function and dynamics. *Pl. Soil,* **71,** 9–21.

Last, F.T., Mason, P.A., Pelham, J. & Ingleby, K. 1984. Fruitbody production by sheathing mycorrhizal fungi: effects of 'host' genotypes and propagating soils. *For. Ecol. Manage.*, **9,** 221–227.

Last, F.T., Mason, P.A., Wilson, J., Ingleby, K., Munro, R.C., Fleming, L.V. & Deacon, J.W. 1985. 'Epidemiology' of sheathing (ecto-) mycorrhizas in unsterile soils: a case study of *Betula pendula. Proc. R. Soc. Edinb.*, **85B,** 299–315.

Linkins, A.E. & Antibus, R.K. 1981. Mycorrhizae of *Salix rotundifolia* in coastal arctic tundra. In: *Arctic and alpine mycology,* edited by G.A. Laursen & J. F. Ammirati, 507–531. Washington: University of Washington Press.

Marx, D. H. 1980. Ectomycorrhizal fungus inoculation: a tool for improving forestation practices. In: *Tropical mycorrhiza research,* edited by P. Mikola, 13–17. Oxford: Clarendon.

Mason, P.A. 1980. Aseptic synthesis of sheathing (ecto-) mycorrhizas. In: *Tissue culture methods for plant pathologists,* edited by D.S. Ingram & J.P. Helgeson, 173–178. Oxford: Blackwell Scientific.

Mason, P.A., Last, F.T., Pelham, J. & Ingleby, K. 1982. Ecology of some fungi associated with an ageing stand of birches (*Betula pendula* and *B. pubescens*). *For. Ecol. Manage.*, **4,** 19–39.

Mason, P.A., Wilson, J., Last, F.T. & Walker, C. 1983. The concept of succession in relation to the spread of sheathing mycorrhizal fungi on inoculated tree seedlings growing in unsterile soils. *Pl. Soil,* **71,** 247–256.

Miles, J. 1985. Soil in the ecosystem. In: *Ecological interactions in soil: plants, microbes and animals,* edited by A.H. Fitter, D. Atkinson, D.J. Read & M.B. Usher, 407–427. (British Ecological Society special publication 4.) Oxford: Blackwell Scientific.

Molina, R. & Trappe, J.M. 1982. Applied aspects of ectomycorrhizae. In: *Advances in agricultural microbiology,* edited by N.S. Subba Rao, 305–324. London: Butterworth Scientific.

Read, D.J., Francis, R. & Finlay, R.D. 1985. Mycorrhizal mycelia and nutrient cycling in plant communities. In: *Ecological interactions in soil: plants, microbes and animals,* edited by A.H. Fitter, D. Atkinson, D.J. Read & M.B. Usher, 193–217. (British Ecological Society special publication 4.) Oxford: Blackwell Scientific.

Richardson, M.J. 1970. Studies on *Russula emetica* and other agarics in a Scots pine plantation. *Trans. Br. mycol. Soc.*, **55,** 217–229.

Slankis, V. 1973. Hormonal relationships in mycorrhizal development. In: *Ectomycorrhizae: their ecology and physiology,* edited by G.C. Marks & T.T. Kozlowski, 232–298. New York: Academic Press.

Swift, M. J., Heal, O.W. & Anderson, J.M. 1979. *Decomposition in terrestrial ecosystems.* Oxford: Blackwell Scientific.

Trappe, J.M. 1962. Fungus associates of ecotrophic mycorrhizae. *Bot. Rev.*, **28,** 538–606.

Trappe, J.M. 1977. Selection of fungi for ectomycorrhizal inoculation in nurseries. *A. Rev. Phytopathol.*, **15,** 203–222.

Tyler, G. 1984. *Macrofungi of Swedish beech forest.* University of Lund.

Vogt, K.A., Grier, C.C., Meier, C.E. & Keyes, M.R. 1983a. Organic matter and nutrient dynamics in forest floor of young and mature *Abies amabilis* stands in western Washington, as affected by fine-root input. *Ecol. Monogr.*, **53,** 139–157.

Vogt, K.A., Moore, E.E., Vogt, D.J., Redlin, M.J. & Edmonds, R.L. 1983b. Conifer fine root and mycorrhizal root biomass within the forest floors of Douglas fir stands of different ages and site productivities. *Can. J. For. Res.*, **13,** 429–437.

Watling, R. 1981. Relationships between macromycetes and the development of higher plant communities. In: *The fungal community: its organisation and role in the ecosystem,* edited by D.T. Wicklow & G.C. Carroll, 427–458. New York: Marcel Dekker.

Watling, R. 1984a. Larger fungi around Kindrogan, Perthshire. *Trans. bot. Soc. Edinb.*, **44,** 237–259.

Watling, R. 1984b. Macrofungi of birchwoods. *Proc. R. Soc. Edinb.*, **85B,** 129–140.

Appendix 1. Specific names, including authorities, of all fungi included in text (excluding those listed in Table 2)

Amanita crocea (Quel.) Kühn. and Romagn.
A. inaurata Secr.
A. muscaria (L.: Fr.) Hooker
A. rubescens ((Pers.) Fr.) S. F. Gray
A. vaginata (Bull.: Fr.) Vitt.
Amphinema byssoides (Pers.: Fr.) J. Erikss.
Cortinarius croceofolius Peck
Hebeloma populinum Romagnesi
H. versipelle (Fr.) Kumm.
Inocybe longicystis Atk.
Laccaria amethystea (Bull.: Merat) Murill
Lactarius rufus (Scop.: Fr.) Fr.
L. tabidus Fr.
L. turpis (Weinm.) Fr.
L. vietus (Fr.) Fr.
Paxillus involutus (Batsch.: Fr.) Fr.
Pisolithus tinctorius (Pers.) Coker and Couch
Rhizopogon luteolus Fr. & Nordh.
Russula aquosa Leclair
R. brevipes Pk.
R. emetica (Schaeff.: Fr.) S. F. Gray
R. fellea (Fr.) Fr.
R. mairei Sing.
R. scotica Pearson
Suillus cavipes (Opat.) Smith and Thiers
S. luteus (Fr.) S. F. Gray
Tricholoma columbetta (Fr.) Kummer