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CURRENT MYCORRHIZAL RESEARCH:

ABSTRACTS OF COMMUNICATIONS PRESENTED AT THE MYCORRHIZA GROUP MEETING, LANCASTER UNIVERSITY, MARCH 28-30 1983

edited by

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FOREWORD

From its conception as the Tree Mycorrhiza Group in Surrey (1979) this third meeting of mainly UK mycorrhizal researchers has seen a considerable degree of evolution. The decision made at the second meeting (Sheffield 1981) to incorporate more non-tree participation and the maintenance of informality in the presentation of papers and discussions (despite the increase in number of participants) has allowed cross-fertilization of concepts and techniques. The group has grown considerably and some statistics showing these changes are given below.

	Surrey 1979	Sheffield 1981	Lancaster 1983
No. of participants	27	35	51
No. of papers read	12	16	15
No. of posters	?	2	11
No. of discussions/workshops	0	1	5
No. of institutes represented	14	15	19

More information is being presented (over 100% increase in contributions since 1979) and is correlated with the increase in number of participants. The 89% increase in number of participants since 1979 (46% since 1981, still maintained an informal atmosphere allowing uninhibited discussion. This was important as for the first time structured discussion sessions were timetabled. Although the number of institutes represented has increased slightly there is a core group of 8-10 institutions which are regularly represented. Does this indicate expansion within existing groups of mycorrhizal research rather than an increase in the number of research groups becoming interested in mycorrhizal work in the UK?

It was very pleasant to be able to have the company of three foreign visitors attending part of the meeting to provide a non-UK viewpoint in the discussions.

Dr. Francis Sanders has kindly agreed to arrange the next meeting at the University of Leeds in March/April 1985.

I wish to thank all participants for their contributions and for helping the meeting to run so smoothly despite the diffuse localities of the lecture theatres.

John Dighton

PROGRAMME

POSTERS

Development of mycorrhizal communities in Sitka spruce

G.W. Thomas, D. Rogers & R.M. Jackson

University of Surrey

The majority of mycorrhizas found on nursery grown Sitka spruce were formed by 'E-strain' fungi. After transplanting the percentage of roots colonized by 'E-strain' fungi decreased and other mycorrhizal fungi, such as *Thelephora terrestris* and *Paxillus involutus*, were found with increasing frequency. Examination of mature sites revealed 21 different mycorrhizal types, 16 in the Alderholt, 11 in the Crychan and 12 in the Glasfynydd. Of the identified mycorrhizal fungi *Thelephora terrestris*, *Lactarius rufus*, *Lactarius tabidus*, *Russula ochroleuca* and *Cenococcum geophilum* were found on all three sites. Sørensens coefficient of similarity revealed that the upland brown earth sites had greater similarity to each other than to the heathland site.

There is increasing species diversity with increasing site age. Most of the fungi, with the exception of the 'E-strain', found in nursery and early transplant sites were also found in mature stands. The'E-strain' appears to be unable to colonize newly formed short roots in the transplant site and it was replaced from existing 'E-strain' mycorrhizas. This replacement may be due to interference competition. Similar replacements, not associated with species exclusion, have been observed in mature stand mycorrhizal communities.

Inoculation of Hardy Ornamentals with V.A. mycorrhizal fungi

S.A. Bowes and T.J. Hall

Glasshouse Crops Research Institute

The size of the container-grown hardy ornamental stock (HONS) sector was discussed and considered to be a likely commercial outlet for vesicular-arbuscular (V.A.) mycorrhizal inoculum in the UK. This is a high value crop (£33.2M in 1982) which includes a large number of potentially endomycorrhizal species. The widespread use, in HONS production, of well-defined growing media, usually peat composts containing controlled release fertilizers, enables more accurate prediction of mycorrhizal development and response to infection than is possible with soil substrates.

Growth-response experiments conducted with soil-less composts and the 'E3' endophyte, thought to be *Glomus fasciculatus*, have given promising results. Rooted cuttings of *Juniperus virginiana* 'Skyrocket', *Juniperus* x *media* and *Magnolia soulangiana* were potted into limed peat: sand containing fritted trace elements and varying amounts of Ficote (16:8:7) controlled release fertilizer. Growth measurements taken after 14-15 months revealed that inoculated plants of all three species receiving 1 gl^{-1} and 2 gl^{-1} Ficote were significantly bigger than their non-mycorrhizal counterparts. At 2 gl^{-1} Ficote the mycorrhizal treatments were significantly better than the uninoculated controls receiving the full rate (4 gl^{-1}). These responses may be attributed, in the main, to improved phosphate and minor element nutrition under conditions when low nutrient levels, because of restricted root absorption area, are limiting plant growth.

The formation of mycorrhizas was also demonstrated at the root initiation stage, using *Escallonia*. No appreciable differences in numbers of plants rooted or weight of fresh root were revealed between mycorrhizal and non-mycorrhizal plants. The requirement of small quantities of inoculum at this stage would make this an ideal method for inoculation, particularly in cases where cuttings are not slow to produce roots.

In addition to improved nutrient uptake, there are a number of other potential benefits of V.A. mycorrhizal inoculation which are applicable to HONS production. These include:-

1. improved tolerance to water stress
2. improved tolerance to pH, soil temperature, toxicants, salinity
3. increased production of cytokinins and other hormones enhancing growth
4. reduced susceptibility to plant disease

The possible commercial consequences of mycorrhizal inoculation were also discussed.

Factors affecting the mycorrhization of Beech by *Hebeloma crustuliniforme* in fertilized peat nurseries

J. Garbaye

Centre de Recherches Forestières de Nancy

An increasing amount of Beech (*Fagus silvatica*) plants in France are grown on peat fertilized with high nutrient levels. They reach plantation size in one year only and are generally not mycorrhized.

The communication deals with the optimization of nursery techniques for artificial mycorrhization of these plants by *Hebeloma crustuliniforme* which seems to be a competitive and growth efficient ectomycorrhizal fungus on most soils where Beech is planted in the north of France. After three years of experiments in routine nurseries, in greenhouse and in growth chamber with vermiculite-peat inoculum, the most important factors prove to be:

- fertilization level. The high nutrient levels currently used in peat nurseries for optimal growth are very unfavourable to mycorrhization by *H. crustuliniforme*. It has to be reduced by at least one half and more for phosphorus. In these new conditions, the growth effect due to mycorrhization compensates the lower fertilization for the final size of the plants.

- inoculation intensity. The mycorrhization level increases with higher quantities of inoculum.

- washing the inoculum improves mycorrhizal establishment, by delaying the death of mycelium as long as receptive short roots are not yet present (4 to 6 weeks).

At the present stage of this research, the best combination of these factors, as a compromise between mycorrhization, size of plants and reasonable consumption of inoculum, is:

- macronutrient level (g m^{-3}): 75 for N, 10 for P, 35 for K

- 5% inoculum (v/v) washed and mixed within the peat

The improvement to the technique will now be looked for in the quality of inoculum (viability in soil) for reducing the quantity needed.

Production and outplanting of ectomycorrhizal Sitka spruce seedlings in Alaska

C.G. "Terry" Shaw

USDA Forest Service

Sitka spruce inoculated at sowing with mycelial cultures of ectomycorrhizal fungi and grown individually in 66 cm^3 containers at two different locations in Alaska have formed ectomycorrhizas. Seedlings were reared in greenhouses maintained for production of containerized seedlings for reforestation use in Alaska. Seedlings currently growing and scheduled for outplanting in May 198 have the following percentages of their short roots ectomycorrhizal with the test fungus mentioned: *Hebeloma crustuliniforme* 89%; *Cenococcum geophilum* 75%; *Laccaria laccata* 94% and *Amanita muscaria* 8.4%. These seedlings will be outplanted onto specific microsites (rotten wood, exposed mineral soil, and undisturbed forest duff) that commonly occur within areas where the natural old-growth forest of Sitka spruce and Western hemlock has been harvested by clear-cutting. Previous plantings on these microsites with non-mycorrhizal Sitka spruce have resulted in overall seedling survival rates of 95%. Thus if any benefit is to be obtained from the planting of seedlings tailored in the nursery with specific mycorrhizal fungi it will likely be in seedling growth. Seedling performance will be closely followed as nutrient analysis indicate that in all three microsites the quantities of available P may be the most limiting nutrient for growth.

Controlled inoculation and growth of Sitka spruce at a commercial forest site.

P.A. Mason, J. Wilson and F.T. Last

Institute of Terrestrial Ecology, Bush.

Recent evidence both from fruit body observations and controlled inoculations have shown that functional differences exist between sheathing mycorrhizal fungi which appear first in the early stages of the fungal succession on young trees and those occurring at a later stage. While both groups of fungi readily form sheathing mycorrhizas with tree seedlings in axenic conditions, only early stage fungi form mycorrhizas with seedlings growing in unsterile soils. These results suggested that the concept of succession has an important bearing on the selection of fungi for inoculating tree seedlings.

As a result, inoculated Sitka spruce seedlings were outplanted into unsterilised forest soils at a site near Hexham, Northumbria. By the end of the first growing season on a peaty gley, heights, on average, had increased from 8.6cm in the uninoculated series to 14.8 and 16.0cm by *Paxillus involutus* and *Laccaria* sp. respectively. On a peat, heights had increased from 11.4 to 14.7 and 17.4cm.

The benefits from inoculating with *Laccaria* sp. were also evident when the populations of seedlings at the peat and peaty gley sites were combined and arranged by height classes. Whereas 83% of the uninoculated controls were shorter than 15cm, the majority (61%) of the seedlings inoculated with *Laccaria* sp. were taller than 15cm.

The evidence to date therefore suggests that, when considering controlled inoculations, that the choice of fungus should be controlled primarily by its position within the mycorrhizal succession and secondly by its ability to stimulate the growth of its host.

Survival of mycorrhizal propagules

Dorothy Spencer and M.J. Daft

University of Dundee

Vesicular arbuscular mycorrhizas (VAM) are ubiquitous in their distribution, being found from polar regions to the tropics and are present in most habitats. They thus can survive under extremes of conditions. The effects of two, temperature and relative humidity, were investigated on the survival of propagules produced by these VAM fungi. The temperatures ranged from 5°C to 45°C and the relative humidities from 13% to 75%. The mycorrhizal propagules were of three types: spores of *Glomus clarum;* hyphae of *G. fasciculatum;* root segments of maize infected with *G. clarum* and root segments of natural bluebells containing more than one endophyte. The relative survival of each propagule type was assessed after storage for several weeks by a dilution technique. The infectivity of the propagules was determined on alfalfa seedlings.

The ability of spores to infect alfalfa seedlings was related to the relative humidity and temperature at which they were stored. Following storage at 45% relative humidity and 5° or 25°C infection occurred from low and high concentrations of inocula, at 35°C from a high concentration only and at 45°C spores did not infect seedlings. Alteration of the relative humidity required higher spore concentrations for infection. Mycorrhizal maize and bluebell segments stored for a short time at 5°C infected alfalfa seedlings but following high storage temperatures maize segments were more successful as inocula. Hyphae did not withstand the storage period.

All propagules caused the severest infection on seedlings following storage at low temperatures.

Regulation of the symbiosis in VA mycorrhizas

D.P. Stribley

Rothamsted Experimental Station

Current evidence suggests that the spread of mycorrhizal infection in a developing root system is a very important determinant of the potential growth response of the host to infection (Sanders *et al.* 1977; work of J. Menge in this laboratory). A clear understanding of the processes which control and affect spread of infection is therefore very important, particularly in relation to annual crops. However, since mycorrhiza are complex symbioses, consisting in effect of one growing organism (the fungus) inside another organism which is itself growing (the hosts' root system), effects of important variables such as the chemical and physical environment, host and fungus genotype, and inoculum density of the fungus, are difficult to interpret without appropriate experimental techniques. One approach we advocate is mathematical modelling. An illustration of the value of modelling is provided by recent work in this laboratory (Buwalda *et al.* 1983) on young leek (*Allium porrum*) plants, where we have shown that the sigmoid progression in time of fractional infection is a simple arithmetical consequence of i) linear growth of individual roots and of the total lengths of infection within them; ii) an approximately exponential rate of production of adventitious roots; iii) a delay of c. 5 days before infection is observed in individual roots.

Modelling should be complemented by detailed, microscopical studies of processes of spread of infection. Information on this topic is very meagre at present.

The study of spread of infection has also been impaired by lack of appreciation of the complexities of whole-plant physiology. We suggest that cause and effect in a complex symbiosis such as mycorrhiza are so inextricably linked that observations on a single variate (e.g. %P in dry matter) may show correlation but will rarely point to causation. Further, many studies have related spread of infection to the concentration in the root of a particular nutrient <u>expressed on a dry weight basis</u>. This is undesirable on two counts. First, recent work at Rothamsted (by R. Leigh) has shown that in many cases it is only the concentration in <u>tissue water</u> that is physiologically meaningful: changes in concentration on a dry weight basis often simply reflect changes in the fresh weight/dry weight ratio (themselves resulting from changes in the thickness of cell walls - perhaps this regulates spread of infection). Second, it is <u>fluxes</u> of nutrients that are likely to be important to the symbiosis rather than the commonly-measured internal <u>concentrations</u>.

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The dynamics of spread of mycorrhizal infection and temperature responses

N. Sheikh

University of Leeds

Knowledge of the dynamics of spread of mycorrhizal infection in plant root systems is crucial if we are to understand the growth response of the host plant. The aim of my work has been to investigate the mechanism of spread of infection.

VA mycorrhizal infection in root systems seems to be built of discrete infection units. Each consists of an entry point originating from a hypha in the soil and associated mycelium in the root cortex. Numbers of entry points increase exponentially with time but the average length of infection units remains nearly constant. We have been able to explain the process of infection spread using simple computer models.

Our experiments in the growth rooms have shown that the rate of spread of infection is sensitive to temperature. We have also studied the influence of soil temperature on mycorrhiza formation in the field. The interaction of soil temperature and mycorrhizal infection will be discussed using data on growth of red clover.

Some Aspects of the Water Relations of VAM Clover Plants

Kay Hardie

University of Oxford

VAM and uninfected clover plants were shown to differ in certain water relation parameters. Infected root systems had greater water conductivity per unit root length when compared with (a) non-mycorrhizal plants grown in the same low nutrient soil and of lower internal root and shoot %P and, (b) non-mycorrhizal plants grown in soil amended with PO_4 and of higher internal root and shoot %P. The increased conductivity is not caused therefore by the greater nutrient status of VAM plants but may be a direct consequence of infection.

Transpiration flux in VAM plants was higher than in uninfected plants when water was readily available but, when transpiration rates were greatly reduced (under conditions of water stress or low light intensity/low temperature) the VAM plants showed a lower flux than control plants. Thus a greater degree of control over water loss is exhibited in VAM plants.

Lower sap osmotic potentials were recorded in some VAM plants which had exhibited lower leaf water potentials than non-infected controls. Analysis of sap for K revealed higher concentrations in the VAM plants but the difference between VAM and uninfected plant sap accounted only for some 8% of the difference in sap osmotic potential observed. Proline levels, often found building up in water stressed plants, were similar in VAM and non-mycorrhizal shoot material. If the ability of VAM plants to tolerate drought is due to the development of low water potential than more work is required to determine the control mechanism.

Discussion session - "Mycorrhizal successions"

Chairman - J.W. Deacon

University of Edinburgh

Intorductory: J.W. Deacon. Successions of sheathing mycorrhizal fungi on birch
L.V. Fleming. Role of mycelial strands in establishment of sheathing mycorrhizas of birch.

In the introductory papers a distinction was drawn between "early-stage" and "late-stage" mycorrhizal fungi of birch, these terms having originally been coined to denote the early or late appearance of fruitbodies of the fungi over a 12 year period on an experimental plot of birches at Bush Estate, Penicuik, Midlothian (Mason *et al.* 1982, For. Ecol. Manage. 4, 19-39). Collaborative work between the Institute of Terrestrial Ecology, Bush, and the Microbiology Department of Edinburgh University was outlined, with special reference to the work of past or present research students, S.J. Donaldson, F.M. Fox and L.V. Fleming. Early-stage mycorrhizal fungi were shown to differ from late-stage in several respects, for example in the ease of establishment of mycorrhizas from basidiospores or vermiculite-peat inocula added to normal, unsterile soil. L.V. Fleming then described his field experiments on coring or trenching of soil to isolate inoculum of mycorrhizal fungi from a food supply provided by the parent tree. He showed that some late-stage mycorrhizal fungi (e.g. *Lactarius pubescens* and *Leccinum* spp.) can infect seedlings planted around parent trees provided that the soil is not cored or trenched. The most plausible explanation of these findings is that at least some late-stage fungi infect seedling roots from mycelial strands or other extra-matrical mycelium which must remain attached to the parent tree (the food base) in order to infect. The suggestion was made in these introductory papers that early and late stage mycorrhizal fungi differ in the inoculum potential required for infection of seedling roots in the mineral soil of the Bush Estate.

A general discussion followed. Support for the concept of succession was provided by Dr. J. Garbaye in his observations of mycorrhizas on oaks. Dr. R. Watling commented that the observed succession at Edinburgh has parallels with the occurrence of different mycorrhizal fungi during invasion of tree-less sites by birch in Scotland: some of the early-stage types are characteristic of pioneer birch woods, whereas the late-stage types tend to occur in closed canopy woodland with a well-developed litter layer. Other contributors to the discussion, notably from Surrey, Merlewood and the Forestry Commission at Edinburgh, noted that there is a transition of mycorrhizal types after outplanting of nursery stock of conifers to field sites. There was some debate as to whether this is a complete replacement or merely a development of a complex 'community'. Anyhow, it seems clear that there are biological differences between sheathing mycorrhizal fungi in terms of establishment and persistence on tree root systems. The

general feeling of the meeting seemed to be that these differences may be exploitable in practice; more information is needed on the respective roles of the rhizoshpere microflora, soil physical factors, nutrient availability and tree physiology (and genotype) as determinants of mycorrhizal establishment.

Much debate centred round terminology. Dr. D. Read and Dr. R. Jackson, in particular, were concerned about the terms 'early- and late-stage' mycorrhizal fungi. The mood of the meeting seemed to be that these terms should be replaced before they become firmly rooted in the literature. "Pioneer" was suggested as an alternative to "early-stage", but no satisfactory replacement for "late-stage" was proposed. It is important to find generally acceptable terms which also denote biological functions, and this is currently receiving attention.

Discussion Session - "Growth Responses and nutrient uptake efficiency in mycorrhizal plants."

Chairman - F.E. Sanders

University of Leeds

Introduction

Our main aim must be to explain the response of the host plant to mycorrhizal infection in a quantitative way. The first requirement is to understand the dynamics of mycorrhizal systems where two or more distinct organisms interact with each other in space and time, in a way much modified by the environment.

Since the system that we are studying changes with time, this must be taken into account. Mathematical models provide one means of doing this and, in addition, serve wonderfully to concentrate the mind.

Host response - the growth of mycorrhizal plants involves feedback. The growth of the host provides space and substrate for the fungus and hence affects the rate at which the fungus can grow. In turn, the growth of the fungus influences the rate of acquisition of nutrients required by the host and hence the growth rate of the host. The following processes are involved:

1) germination of propagules and hyphal growth in the soil
2) the initial infection process
3) development of the mycorrhiza
4) spread of the fungus to other parts of the root system to form other mycorrhizas
5) the transfer of host assimilates to the fungus
6) the growth of fungal biomass and its partition between mycorrhiza and soil
7) uptake of water and mineral nutrients from the soil. Their transfer to the host through the mycelium
8) the influence of altered nutrition of the host on its growth rate and the partitioning of assimilates
9) the effect of a change in the growth rate of the host root on the space and substrate available to the fungus, and hence on the growth of the fungus itself.

All of the above has assumed one host and one fungus. The situation in reality is far more complicated. Many fungi may compete to find a home in one root system. Many plants may also compete with each other for space and nutrients.

VA mycorrhizal fungi and crop plants - much progress has been made in understanding this situation, particularly by the use of models. The more complex case of ectomycorrhizas is less well understood. There seems to have been much emphasis placed on 'natural history' but much less on host responses and the dynamics of the symbiosis. It is usually reckoned that trees need their mycorrhizas but questions of 'how much' and 'which' may not have been satisfactorily answered.

Discussion at the IUFRO meeting last year in Edinburgh centred on the question of 'efficiency' in mycorrhizal fungi. Nobody seemed to be able to define exactly what this means. The advocates of inoculation with 'elite strains' of mycorrhizal fungi as the answer to the problems of the farmer or forester tend to consider as efficient those particular inocula which seem to do exactly what they want. Unfortunately, the spectacular responses that can be obtained in pots may not be easily repeatable, particularly in the field! Ecologically-minded mycorrhizasts point to evidence of succession in fungal populations with the implication that different fungi are most efficient at different stages in the growth of a forest or the evolution of a piece of arable land. Some would maintain that the clue to the definition lies in biochemical subtleties or even in taxonomy. Whatever one's views, a clear definition of 'efficiency' could be very helpful.

Perhaps the definition lies merely in a consideration of profit and loss. If we are in a position where mycorrhizas are important to the growth of a crop and we need to compare one fungus with another, in the short term, the most efficient fungus must be the one that leads to the largest yield. This conclusion however takes no account of varying difficulty in handling various organisms. For example, some species of VA mycorrhizal fungi are profligate producers of spores in greenhouse pot culture and hence are easy to handle. Others may not produce spores at all and are handled with extreme difficulty. How can profuse sporulators be compared with species which produce few or no spores? In the case of ectomycorrhizal fungi, the great majority of species cannot conveniently be cultured. It is easy to see why so little attention has been paid to some of the commonest species of woodlands.

In comparisons between species of mycorrhizal fungi in screening trials, it is clear that attention must be paid to the provision of equivalent doses of inoculum. This seems to be a very difficult problem. Should inocula be compared on the basis of viable propagule numbers? If so, how can these be measured? Alternatively it may be better to compare fungi after they are established in the root system, on the basis of subsequent effects on the growth of the host. In this case saturation doses of inoculum could be used, followed by growth analysis and measurement of the rate of acquisition of nutrients by the host plant. If the growth of the host depends on nutrient uptake, a measure of efficiency can then be obtained by calculation of the rate of uptake of nutrient per unit of mycorrhizal tissue, and comparing this with rates of uptake by other types of mycorrhiza, or nonmycorrhizal root, under the same conditions.

In the long term, an 'efficient' mycorrhizal fungus selected in screening trials must be able to persist in the field in competition with the indigenous population. Profuse sporulators or those fungi with a high rate of vegetative spread may have the advantage in this respect, but such capacities may not necessarily be correlated with superiority in terms of ability to aid the growth of the host plant.

In summary, an 'efficient' mycorrhizal fungus should perhaps have the following spectrum of attributes:

1) it should establish rapidly on the host root system after inoculation
2) it should greatly increase the inflow of mineral nutrients to the root system while costing its host little in terms of diverted assimilates.
3) it should have the ability to prevent the establishment of other, less desirable, fungi in the root system.
4) it should be able to persist for several seasons.

I hope that these contentions (and omissions) will be critically dealt with during the discussion!

A comparison of two methods to assess comparative nutrient uptake efficiency by sheathing mycorrhizas

J. Dighton

I.T.E. Merlewood Research Station

Direct uptake from ^{32}P-labelled phosphate injected into a nutrient deficient peat growth medium by differentially inoculated *Pinus contorta* and *Betula pubescens* seedlings was compared with a bioassay technique for assessing phosphorus deficiency in plants (Harrison and Helliwell 1979).

Good correlation existed between the two techniques for measuring rates of P-uptake in birch, but not so for pine, where the bioassay appeared to be relatively insensitive. Neither method of determining phosphorus uptake correlated well with P-concentrations in any of the plant parts.

In birch *Hebeloma saccharoliens* causes a significant increase in P translocated to the shoot than the non-mycorrhizal control or any of the other mycorrhizas tested. *Suillus luteus* caused a similar significant effect in pine with up to four times the amount of ^{32}P reaching the shoot in 24h than other treatments.

Although the data is in a preliminary stage of analysis, it would appear that the injection technique is more sensitive than the bioassay. Even in this nutrient impoverished peat substrate different mycorrhizal fungi are shown to have differing effects on the rate of uptake of phosphorus and may influence its distribution within the plant host.

Reference

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The ultrastructure of sclerotium-like bodies of *Hebeloma sacchariolens* and their role as inocula of *Betula pendula*.

F.M. Fox

I.T.E. Bush Estate

Mycorrhizas formed artificially or naturally between *Hebeloma sacchariolens* and birch are frequently associated with white, sclerotium-like bodies; the ultrastructure of these bodies was investigated, as was their possible role in dormant survival.

Ultrastructurally, the sclerotium-like bodies consist of a narrow outer zone of vegetative hyphae with thin walls, merging progressively into a pseudoparenchymatous tissue composed of large cells with thick, striated walls and filled with osmiophilic material presumed to be lipid. These structures therefore have quite the opposite ultrastructural appearance to that of sclerotia of most root-inhabiting fungi, in which an outer zone of thick-walled cells characteristically enclose an inner zone of thinner walled cells. Nevertheless, when retrieved from soil after 9 months burial, the sclerotium-like bodies of *H. sacchariolens* were able to initiate infection of birch seedling roots, suggesting that they have a survival function. Ultrastructural investigation of such buried sclerotium-like bodies revealed invasion of the surface regions by several micro-organisms, though the central regions remained intact; air-drying before burial markedly increased apparent susceptibility to microbial invasion, as is also reported for some sclerotia of plant pathogenic fungi.

Ultrastructural features of sclerotia of *Paxillus involutus* and *Cenococcum graniforme* revealed a more normal sclerotial-like organisation but interestingly, the sclerotia of *P. involutus* buried for 3 months, showed a much greater degree of microbial attack than did the sclerotium-like bodies of *H. sacchariolens*.

Differential growth responses of mycorrhizal Sitka spruce seedlings in sterilized and unsterilized forest tree nursery soil

C. Walker

Forestry Commission, Roslin

Sitka spruce seeds were sown in a greenhouse in pots of soil from a forest nursery on a fertile, old agricultural site. The soil in half the pots had been sterilized with 5.4 Mrads of gamma irradiation.

Twelve seeds were sown, and after emergence all but two were removed. When these seedlings were well established (91 days after sowing), a fungal treatment was applied. The treatments were based on *Laccaria proxima* or *Thelephora terrestris* mycelium grown in a liquid medium by N Plummer (a CASE student under the auspices of the University of Surrey and Tate and Lyle PLC). The mycelium was filtered onto a fine sieve (45 µm), thoroughly rinsed in tapwater, and then re-suspended in fresh tapwater. Half of the suspension was then filtered through Whatman No 3 filter paper and then through a 2 µm Millipore filter to provide a mycelium free control. The five treatments therefore consisted of:-

1. *Laccaria proxima* mycelial slurry
2. Fungus-free filtrate from 1
3. *Thelephora terrestris* mycelial slurry
4. Fungus-free filtrate from 3
5. Tapwater control

Each plant in a treated pot received 10 ml of the appropriate treatment, injected into the root zone through a sterilized laboratory cannula (2 mm) from a sterile syringe. There were 10 replicates of each treatment.

Destructive analysis was carried out 165 days after inoculation. The mean height growth was measured and results subjected to analysis of variance. There was no treatment - sterility interactions and there were distinct differences, significant at the 95% level, among treatments. Differences were located by use of Student's t tests between means. *Laccaria* and *Thelephora* both enhanced growth (equally) on the sterilized soil. Sterilizing the soil yielded a significant height increase, though the two fungi improved growth yet further. Neither of the fungi increased height growth on the unsterilized soil. The fungus-free filtrate did not enhance growth over the relevant controls on either sterile or non-sterile soil.

The conclusion drawn from this experiment, admittedly in potted plants in a greenhouse, is that only in sterilized soil was the introduction of mycorrhizas beneficial to height growth.

Glomus fasciculatum: A Taxon misunderstood!

C. Walker

Forestry Commission, Roslin

Glomus fasciculatum is cited more often in published work on endomycorrhizas than any other species, and yet it is one of the least well understood taxa in the Endogonaceae. Thaxter's original description was confounded by an unfortunate juxtaposition of sporocarps giving the erroneous impression that zygospores and chlamydospores were present in the type collection (Thaxter 1922, Gerdemann 1965, Gerdemann and Trappe 1974). Gerdemann (1965) described a sporocarpic, chlamydosporic isolate in the Endogonaceae to redescribe the species, and designated part of Thaxter's type material as a lectotype. Later, Gerdemann and Trappe (1974) expanded the species concept even further, and it is in that sense that the majority of identifications are now made.

Since 1973 I have been collecting and examining material that could be, or has been, classified as *G. fasciculatum* sensu Gerd. and Trappe, and it is now clear that this species concept is too broad, and that it encompasses several morphologically different taxa. Some of these, eg *G. etunicatum*, *G. intradices*, and *G. invermaium*, already have been separated into different taxa whilst others are as yet undescribed. Yet others can be considered to be *G. fasciculatum* in the sense probably intended by Thaxter and represented by the lectotype material. The following fungi have been sent to me identified as *G. fasciculatum*. Many had been used in mycorrhizal research, and had been identified as such in publications:

G. claroideum
G. desertícolum
G. etunicatum
G. intraradices
G. invermaium
G. macrocarpum
G. microcarpum
G. occultum
G. leptotichum
G. pallidum

plus the Rothamsted 'E3' organism and several other undescribed taxa.

Among the material I have examined, were the type specimens from the Farlow Herbarium (kindly loaned to me by the curator). From examination of these it has been possible to observe characteristics not noted by previous workers, that allow a more precise definition of the taxon, and it is clear that the species, far from being common as implied in the literature is relatively rare. However, certain recent collections from Rhode Island, USA, and other pot-cultured isolates from California, quite clearly are the same organism as the lectotype of *G. fasciculatum*.

The characteristics that define *G. fasciculatum* sensu stricta are spore size (60-85 X 60-70 µm), a thick laminated inner wall (6-14 µm thick), a thin, persistent, tightly adherent, hyaline outer wall (≤ 1 µm), and light yellow to very pale yellow-brown colour. Isolates used in studies should be carefully examined and the epithet *fasciculatum* should be used only for specimens that correspond with this description.

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Effects of waterlogging on Scots Pine seedlings and their mycorrhizas

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As part of a larger field survey of the distribution of fine roots and mycorrhizas of Scots pine on a peat bog subjected to waterlogging at different water-table depths, a laboratory experiment to monitor the effects of waterlogging on mycorrhizal inoculated Scots pine seedlings was set up. Seedlings of Scots pine (*Pinus sylvestris* L.) were inoculated with the following fungi

Control (no fungus) (C)
Hebeloma crustuliniforme (HC)
Suillus luteus (SL)
Paxillus involutus (PI)

and planted in groups of 4 like mycorrhizal types in each of 4 replicate root observation chambers containing a 1:2 mixture of sand and Kirckonnell Flow peat.

Sets of 4 replicate chambers were subject to waterlogging with water tables at the following depths below the surface

0 cm
0-5 cm
5 cm
15 cm

(depth altered at 2 week intervals)

After 2 months growth under artificial light at 20°C the plants were washed free from the peat:sand mixture and root length, percentage mycorrhizal infection, top height, top N- and P- contents and peat:sand N- and P-contents were assessed.

Data suggests that:

1) Waterlogging suppresses seedling growth.

2) Inoculated seedlings tend to have less mycorrhizas when relieved of waterlogging pressure than those subjected to waterlogging. This is particularly evident in *Hebeloma*.

3) Seedlings inoculated with *Hebeloma* and *Suillus* maintained a higher number of mycorrhizas than control or *Paxillus* seedlings under waterlogged conditions.

4) Under waterlogging conditions nitrogen availability appears to be the limiting factor to plant growth. NH_4-N appears to be available at 0-5 cm and 5 cm and 15 cm water table depths but uptake is inhibited, except at the 15 cm depth.

5) Plant weight and nitrogen content are correlated to the degree of mycorrhizal infection of the root.

Popular Mycorrhizas: A new method for the synthesis of poplar mycorrhizas under sterile conditions.

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A study of the interaction between mycorrhizal fungi and poplar roots was undertaken. Possible symbionts were isolated from roots of Poplar or sporocarps of basidiomycetes growing adjacent to roots. Sterile plantlets were obtained from surface sterilized internodes of Populus hybrid TT32. Roots were characterized according to the method of Dominik. after 8 weeks mycorrhizas formed between Poplar roots and *Hebeloma truncatum* and *Thelephora terrestris*.

Do Collembola graze mycorrhizas?

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Field sampling and laboratory experiments are being set up to determine collembolan population size and composition under differing aged stands of *Pinus contorta* and to assess their impact on nutrient uptake via mycorrhizas.

Preliminary choice feeding experiments show that two commonly occurring collembola prefer the mycorrhizal fungus *Paxillus involutus* than the saprophytic *Marasmius androsaceus* ($P < 0.01$). Both collembolan species significantly avoid *Hebeloma crustuliniforme* ($P < 0.05$).

Mycorrhizal infection of birch and sycamore in relation to plant and soil variables

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Seedlings of birch and sycamore raised from several seed-lots were grown in a pot experiment on a range of 25 Cumbrian soils (pH 3.2-7.9; organic matter content 7.5-88.8%). Mycorrhizal infection and its intensity were measured after 2 years growth and compared with plant size and a large number of soil variables. The soils were maintained in the fresh field state and were not inoculated.

Percentage frequency of birch ectomycorrhizas was recorded 'macroscopically' (x5) by examining the external morphology of the roots. These were later termed 'mature' when examination of squashes of the supposed non-mycorrhizal roots (x375) revealed sheaths and Hartig nets in various stages of development. We had no information on the physiological state of these mycorrhizas, but significant correlations between infection and certain soil/plant variables showed up only in the data from 'immature' mycorrhizas which could have important practical implications for other mycorrhizal workers.

Data on the V-A mycorrhizal infection of sycamore were shown for comparison. In both species, the most unexpected correlations occurred between infection and extractable iron.

Invasion of VAM spores by soil micro-organisms

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During investigations of the natural occurrence and effect of agricultural practices on VAM spore populations and infection of crops in Southern Israel and South-East England, we have noticed that many spores show evidence of penetration and colonization by other soil micro-organisms. Two VAM spore types in particular consistently possess penetration canals, namely strains of *Glomus constrictum* and *G. macrocarpum*.

Papilla-like ingrowths from the inner surface of the spore wall often develop at the base of these canals, in an analogous way to the lignitubers of invaded plant cells. In surface view, the papillae appear as circular deposi around the central radial canal. Examination of spores in the SEM reveal the presence of many circular penetration holes approximately 1-2 µm in diameter (i.e. generally smaller than those formed as a result of amoeboid attac on other fungal spores in soil). In some cases, fungal hyphae have been observe growing through the canals, and we suspect that these are the causal agents. In spore sections, the papilla-like deposits can be seen on the inner surface of the spore wall. Numerous types of hyphae and zoosporangial structures have also been seen within these two VAM spore types but as yet remain unidentified. On plating out of apparently healthy, surface-sterilized spores of both Israeli and Kentish strains of *G. mosseae* and *G. caledonium* on weak nutrient agars, similar types of non-sporulating, aseptate hyphae have been observed. In some examples, the presence of such mycelia originating from within the VAM spore has not prevented its own subsequent germination.

Physiological variation in isolates of *Boletus subtomentosus*

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The proven mycorrhizal species *Boletus (Xerocomus) subtomentosus* L. ex. Fr. (Melin, 1925; Vozzo and Hacskaylo, 1962) has been shown to rapidly degrade leaf litter and produce polyphenol oxidases as actively as many white rot fungi.

Two different physiological races of *B. subtomentosus* were described by Lundeberg (1970); one a mycorrhizal race having slow growth and low enzyme potential, and the other resembling litter decomposing fungi with rapid growth and high enzyme potential. Further work by Lindeberg and Lindeberg (1977) and Giltrap (1982) has confirmed the existence of different physiological strains.

To understand the processes regulating ectomycorrhizal formation, and in particular the question of specificity, the physiological differences amongst hosts and between the fungal symbionts must be investigated with focus on the intraspecific level.

A collection of *Boletus subtomentosus* isolates is being gathered, with twelve isolates collected to date (donations always welcome!).

The results reported are from initial experiments to determine the extent of variation in the physiology of the isolates of *Boletus subtomentosus* collected. It can be seen that there is a wide range of variation in the behaviour of the isolates on gallic acid agar, lignin agar, carbon source utilization, growth rates and performance in pure culture synthesis tests.

The real interest now lies in determining how these differences between isolates affect their performance in forming mycorrhizas, the efficiency of the different mycorrhizas, and what differences between isolates controls their ability to produce mycorrhizas.

Future and current work -

More detailed study of Carbon source utilization.
Examination of Nitrogen source preferences.
Production of Acid Phosphatase in vitro.
Assaying Pectinolytic abilities of isolates.
Carbohydrate analysis of the synthesized mycorrhizas produced by different isolates.

Methods for mycorrhizal polyphosphate studies

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A brief outline of work in the mycorrhizal field on polyphosphates was given. The main areas where technical problems had hampered research, and our solutions to them, were illustrated. They were as follows:

(A) Colorimetric P determination in the presence of labile phosphate esters.

A new method was detailed which offers the high accuracy of present techniques, whilst minimising interference due to hydrolysis, by carrying out the assay at pH 4.7.

(B) Extraction of phosphate fractions and separation of poly-P's from them.

Our extraction sequence, using various buffers to give stable extraction conditions, and washing steps to minimise carry-over of P between fractions was outlined. Poly-P's were separated from these fractions by ethanol precipitation. This method allows isolation of 5 Poly-P types that appear to possess different physiological activities and occupy unique and separate intracellular sites.

(C) Manipulation of mycorrhizal material.

Routine methods i.e. sequential suspension and centrifugation of material, are tedious slow and liable to errors due to imperfect separation of supernatant from pellet. 'Two-way syringes', used by us for extraction procedures were demonstrated. They offer high control of extraction environment in a sealed system, and total separation of filtrate from homogenized mycorrhizal material. This allows large numbers of samples to be processes simultaneously, where practical considerations had previously limited experimental size to 4-6 samples, hence greatly increasing the scope for experimental design.

Illustrative results showed that uptake from 0.16 mM $KH_2{}^{32}PO_4$, in order of decreasing importance, was into (a) P and soluble sugar phosphates, (b) the two acid soluble polyphosphate fractions, (c) the pH9 Poly-P, (d) the pH12 Poly-P. Incorporation into all other fractions was negligible i.e. less than 2% total incorporated in each fraction.

The Ultrastructure of the host-fungus interface in ectomycorrhizal associations

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In ectomycorrhizas two distinct types of interface are found in compatible associations between the Hartig net and host cortical cells. The first type of interface simply involves direct contact between the host cell wall and the wall of the Hartig net, both walls remaining distinct. In the second type of interface the outside of the host cell wall adjacent to the Hartig net and to a lesser extent the wall of the Hartig net itself becomes indistinguishable from the matrix or involving layer, in which the Hartig net appears to be embedded. Both modified and unmodified interfaces are found in both ascomycete and basidiomycete associations and it is probable that the modified interface is a feature of mature mycorrhizas while the unmodified type is found only in young developing mycorrhizas. Histochemical evidence from both light and electron-microscopy suggest that this involving layer is very similar to host primary cell wall material.

In compatible ectomycorrhizal associations where there is no physiological imbalance, the development of the interface remains remarkably constant regardless of the species of host or symbiont. The development of the interface may be altered by the compatibility and physiological state of both symbionts and also by prevailing environmental conditions. For example the presence of high glucose levels in in vitro syntheses can induce changes in this interface including thickening of the host cell wall, the formation of root cell wall ingrowths and the deposition of electron dense particles within this wall.

Host and fungal plasmalemmas are also essential components of the interface and present research is concentrated on the localisation of membrane bound enzymes, especially ATPase and phosphatases in this area. These enzymes may play an important role in the bidirectional flow of molecules and ions across the interface.

Inter- and intra-specific transfer of carbon between mycorrhizal plants in light and shade

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Germination involves the mobilization and consumption of assimilate reserves in the seed, the quantities of which are progressively reduced as seedling development proceeds. Successful establishment of the seedling will therefore be dependent upon the renewal of the assimilate supplies.

However, germination in the natural environment frequently occurs in shade cast by the canopy of mature plants. Under these circumstances the capacity to obtain assimilate supplies from photosynthesis may be restricted and alternative sources may be of great importance. It is known that seedlings germinating in closed plant communities rapidly become mycorrhizal as their roots contact hyphae or infected roots of the established plants.

We have investigated the possibility that mycorrhizal interconnections may provide pathways through which assimilates will pass along a concentration gradient from fully illuminated adult plants to shaded or unshaded seedlings grown in intra- and inter-specific associations.

Distribution of radioactivity (dpm mg^{-1} dry wt) in mycorrhizal (M) and non-mycorrhizal (NM) sink seedlings of *Plantago* and *Festuca* grown in the shade (S) or unshaded (US) after exposure of leaves of *Plantago* source plants to $^{14}CO_2$

		MS	MUS	NMS	NMUS
Plantago	shoot	42	568	49	183
		436	809	103	233
		352	950	41	863
	root	20839	4456	752	471
		55372	6767	927	390
		208597	11086	319	1849
Festuca	shoot	519	483	11	133
		917	596	235	72
		562		50	261
	root	143069	15927	1089	412
		89427	12809	746	392
		97444		1185	669

(values are means of three replicates)

The results indicate that assimilates can pass from plant to plant through interconnecting hyphae. We may conclude therefore that the assimilate requirements of the seedlings may be satisfied at least to some extent by transfer from mature established plants. This transfer is more effective in shaded conditions.

Mycorrhizas and heavy metal resistance in the Ericaceae

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It seems likely that many plants growing in heavy metal polluted environments are mycorrhizal, yet very few studies have been done on the role of the mycorrhizal fungus in heavy metal resistance.

Parys Mountain, Anglesey is a disused copper mine which has been colonized almost exclusively by *Calluna vulgaris*. Analyses of field material showed that there were significantly higher levels of Cu in both mine spoil and vegetation in comparison with a control, unpolluted heathland.

The mycorrhizal fungus was isolated from the roots of Parys *Calluna* seedlings and cultured 'in vitro'. The Cu-resistance of the isolate was assessed by inoculating flasks containing a series of Cu concentrations in liquid medium and harvesting the mycelium at intervals. Two other ericoid endophytes and two ectomycorrhizal fungi were tested in the same way. It was found that all the ericaceous endophytes were more resistant than the ectomycorrhizal fungi and that there was very little difference between the growth response of the Parys endophyte and *Pezizella ericae* (ericaceous endophyte from a control site).

A study of the Cu resistance of the higher plants in the non-mycorrhizal (NM) state showed that after a period of growth Parys *Calluna* contained significantly lower Cu concentrations in roots and shoots than *Calluna* from the control site. The ability of the Parys endophyte and *P. ericae* to provide resistance was tested. There was no significant difference between the Cu concentrations, in the roots and in the shoots, of Parys and control *Calluna* when infected with either their own endophyte or that of the other race of *Calluna*. Mycorrhizal plants had significantly lower Cu concentrations than NM plants.

In summary, there is some evidence for a degree of resistance already present in the endophyte and an exclusion mechanism evolved by Parys *Calluna* in the NM state. However, the main reason for the success of *Calluna* on metal polluted sites is probably largely attributable to its mycorrhizal status.

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