

MEET THE GLOMALES – the ecology of mycorrhiza

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Meet the Glomales

The role of lower organisms in both natural and man-made ecosystems is grossly underestimated. They go un-noticed because they are too small to see or they live in the dark, impenetrable world of the soil. Worse still, inestimable numbers of species are unculturable so that it is impossible to discover their biology in the laboratory. Some, maybe very many, have yet to be detected. There are so many organisms about which we know little or nothing, and we deny their ecological importance and disrupt their environment at our peril.

An individual such as this author cannot have sufficient knowledge to discuss authoritatively the interactive ecology of all lower organisms in the countryside, but authors with expertise in other disciplines may wish to add to what is a wide-ranging debate, influenced by what I have to say. However, I am one of the few who do know something about the Glomales, an obscure group of fungi that play a significant part in all natural ecosystems. As far as we can tell they are exclusively symbiotic organisms living in association with plant roots to form what is variously known as ‘vesicular-arbuscular mycorrhiza’ or ‘arbuscular mycorrhiza’, but what I prefer to call ‘glomalean endomycorrhiza’ or GEM.

Any ecological threat to lower organisms, in particular those involved in symbiosis, is likely to have serious knock-on effects on other organisms within a community. However, such changes are not obvious enough to affect the entrenched ways of gardeners, farmers and foresters, developed during the thousands of years since the invention of land management.

We do not have demographic data to illustrate threats to these fungi because the necessary foundation of such an exercise, the taxonomy, is uncertain, and there are too few people studying them to carry out a meaningful survey. What we have discovered recently about the ecology of mycorrhiza raises points that ought to affect the thinking of all concerned with protecting the miserable remains of the British countryside and, if it can be achieved at all, its reconstruction.

Here is further evidence (as if we needed more) that we cannot hope to recover what is lost to agriculture, industry and development, and that ambitious attempts to restore damaged communities to their original condition are unrealistic. Once destroyed, their complex, interactive integrity is lost and they are gone forever.

Immortal, invisible . . . *inscrutable*

When the word ‘fungus’ is mentioned, the mind immediately conjures up images of field mushrooms, fly agarics, fairy rings and brackets. These represent but a small part of organisms whose wide-ranging bulk remains unseen and unappreciated below ground or lurking in rotting logs until they declare their presence by producing visible fruiting bodies in order to sporulate (Rayner 1993). I do wish naturalists would stop calling mushrooms and toadstools ‘fungi’ with barely a thought for the rest of the organism *and* the majority of fungi that do not form mushrooms.

Several distinct groups of fungi associate in symbiosis with plants for, it is often said, their mutual benefit. It's not quite that simple - nothing in ecology is simple! - but to save us a long and convoluted discussion, the idea of the partners in symbiosis helping each other in a reasonably balanced fashion and surviving the interaction will do for now.

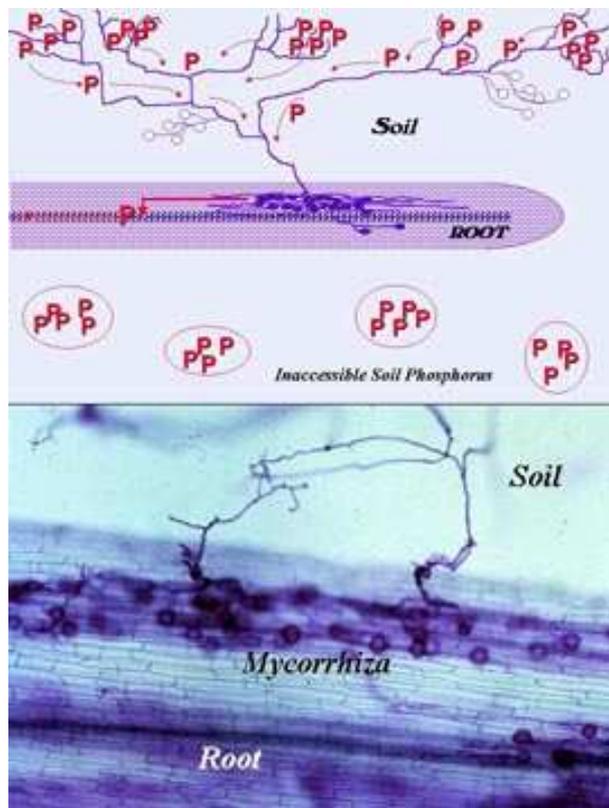


Figure 1. Above: Diagram of a glomalean endomycorrhiza showing the pathway of phosphorus from soil to plant (x ~100). Below: Photomicrograph of a bluebell mycorrhiza (x 400); the root is colonised by a species of *Glomus*.

The symbiosis we call mycorrhiza, a conflation of two Greek words simply meaning fungus-root, is best described by Smith & Read (1997). In terrestrial communities mycorrhiza has always been a dynamic functional feature in which specialised soil fungi invade plant roots where they proliferate to form an interface for nutrient exchange between the parties in the symbiosis (Figure 1). It might be new idea so to us, but to the living world this is old hat. Fungi of the order Glomales first associated with plants when they were still aquatic, and together they invaded the land, nearly 500 million years ago. Indeed, these fungi, or rather the symbiosis, probably facilitated plant life on land. This remarkable history is supported by

both the fossil record (Pirozynski & Malloch 1975) and molecular sequences (Simon *et al.* 1993).

Today an estimated 90% of the world's plant species are

mycorrhizal. The few that are not have subsequently evolved a variety of ingenious ways of doing without. Mycorrhiza is ubiquitous, occurring in all plant communities on every continent, even Antarctica.

Mycorrhizal fungi form highly branched, wide ranging, interconnected networks that explore the soil in which they live for nutrients, invading roots of favoured plants in order to obtain a supply of carbohydrate. They are unable to manufacture their own carbohydrate by photosynthesis or decomposition of organic matter. Well, they don't need to bother because in natural communities they live the easy, untroubled life they have enjoyed for the past five thousand millennia. Carbohydrate is readily available when they care to collect it *via* plant roots, and plants produce excess so that they can divert as much as 20% to the fungal fund. There are a number of mycorrhizal plants that do not have chlorophyll (e.g. achlorophyllous orchids), and the relationship might be quite single-sided; indeed the host may well be considered to be parasitic on its partner as it obtains all of its carbohydrate *via* the fungus and apparently provides nothing in return (there is bound to be more to it than that). However, most plants are

green and they produce plenty of carbohydrate, some of which can be, and is, fed to or collected by their mycorrhizal partners.

When in roots, mycorrhizal fungi are able, if it suits them, to return favours by benefiting their host in some way, usually by converting organic to inorganic nitrogen (in peaty heathland soils nitrogen is unavailable) or foraging for phosphate on behalf of their hosts (an essential nutrient which is immobile in mineral soil: difficult for many plants to

obtain, but a doddle for the right fungi). They can also confer some degree of pest, disease or drought resistance (Gange & Brown 1997 and Figure 2).

Any plant may form numerous different mycorrhizas and a fungus may choose to associate

with any combination of plants. Therefore, some mycorrhizas can be functionally different from others when they vary in the identity of their fungal components, and in the way they interact with the plant and each other in space and time.

There are two distinct classes of mycorrhiza. The *ectomycorrhizal* fungi ensheath roots but do not invade root tissue, and many produce recognisable mushrooms. The *endomycorrhizal* fungi actually enter root cells to exchange nutrients, with no adverse effect on the plant, and they cannot be seen at all without a microscope.

Ectomycorrhizal fungi are of vital importance to many plant species, especially forest trees in temperate regions, and no forest ecosystem would function properly, if at all, without them (Rayner 1993). However, the majority of the world's plants, perhaps 75% or more, associate with fungi of the zygomycete order Glomales of which only 150 remarkable if invisible 'taxa' have been discovered (Morton 2001). As far as we know they are asexual and the mycelium grows indefinitely. They are arguably immortal. They do not conform to our conventional notion of 'species' and there may actually be many more than 150 of them, segregated by functional or genetical characteristics within morphologically distinct species. To date it has been impossible to culture them *in vitro* and they always have to be grown in association with living plant roots, requiring techniques that are far from easy to manage. Culture and experimentation are fraught with problems and, it is becoming uncomfortably evident, the behaviour of these fungi in the laboratory is often very different from the way they behave in nature. Some species are amenable to glasshouse culture whilst many others frustratingly refuse to co-operate, often those which show signs of having ecological importance in field studies! (Merryweather *et al.* unpublished)

Benefit from Mycorrhiza (GEM)

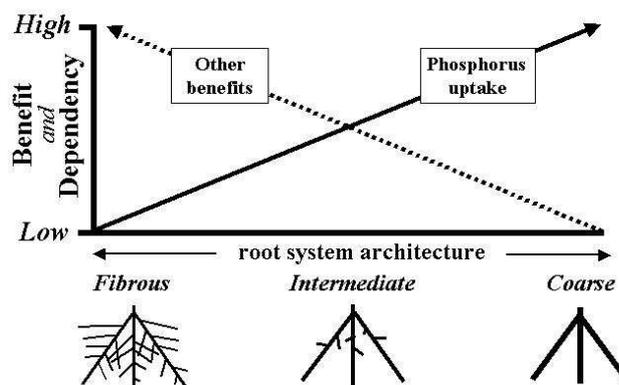


Figure 2. Model showing the interaction of a plant's benefit from and dependency upon glomalean endomycorrhiza depending upon root architecture. The fibrous root type is found in e.g. poaceae, cyperaceae, brassicaceae, the coarse root type is found in e.g. liliaceae, amaryllidaceae, magnoliaceae. Intermediate is less easily defined. Redrawn after a figure in Newsham, K K, Fitter, A H & Watkinson, A R, 1995 Multi-functionality and biodiversity in arbuscular mycorrhizas. *TREE* 10(10): 407-411.

Foundation of natural communities?

Despite being fiercely independent, unpredictable, devious, perhaps in a way 'intelligent' beasts, glomalean fungi ultimately rely upon plants for their existence. Equally, plants and plant communities depend upon their symbiotic fungi. I trust the reader has by now begun to realise that mycorrhiza probably plays a fundamental role in plant community dynamics, and that anthropogenic disturbance of any community might result in loss of not only the trees, flowers, birds and giant pandas, but also the unseen, little known or even undetectable organisms which could underpin community structure (van der Heijden *et al.* 1998).

The natural community in which the role of mycorrhiza has received a lot of research attention is English woodland (e.g. Merryweather & Fitter 1998a; Helgason *et al.* 1999) and this has been compared with the situation prevailing in arable land, which has often come into being as the result of woodland destruction. Woodland soil is the more productive (acknowledged, it produces little usable food for humans), yet from the human viewpoint it is, like soils of all self-sustaining natural ecosystems, considered to be infertile. To be of any use to man, soil has to be cleared of all plants and ploughed, rotavated and harrowed until it is completely crumbled, mixed and homogeneous - utterly unlike any natural soil. Mechanical maltreatment alone is enough to compromise biological soil functioning, as many of the organisms that enabled it to be fertile when it was undisturbed are broken up, desiccated, evicted: unable to survive (Merryweather & Fitter 1998b). Next, therefore, soil fertility has to be increased by the artificial addition of nutrients. Supplied with everything they need, many crop plants may have no use for dependent indigenous micro-organisms, which die. Many crop plants are grown in monoculture, reducing the diversity which soil micro-organisms usually have available for interaction, so those that form specific symbioses must die. Some crop plants (e.g. rape, sugar beet) are non-mycorrhizal, so during their growing season there is no support for mycorrhizal fungi, and the fungi die. Remember that the Glomales require plant hosts for their supply of carbohydrate (Figure 3). These fungi do produce spores, but in many species they seem to be of little value as propagules.

Once the structure of soil and a significant proportion of its community of organisms have been destroyed the soil loses its ability to function the natural, economical way by recycling. Nitrates are highly soluble and, as we well know, excess flushes away to pollute watercourses. Although soluble, phosphates are immobile in soil, electrically attached to clay particles. Many plants have coarse roots and are unable to forage for phosphorus without fungal assistance (Figure 2). If populations of glomalean fungi are reduced or absent, then the phosphate accessible to inefficient, non-mycorrhizal roots is soon used up and more must be added, increasing the soil pool of unavailable P. Fertiliser must be added: more and more of it until the soil is thoroughly overloaded, yet plants cannot get at it and much of it goes to waste or it accumulates compounding the problem.

Crops grown in monoculture become susceptible to massive attack by pests and pathogens, so toxic chemicals are added to the system in the form of all sorts of pesticides which in their turn will kill not just the desirable birds, bees and ladybirds, but numerous sensitive but inconspicuous soil organisms such as the mycorrhizal fungi, which in their turn could have been helping to fend off the very pests and diseases against which those toxins were targeted (Newsham, Fitter & Watkinson 1995 and Figure 2).

Enriched but impoverished

Arable soil - or, rather, the inert, crumbly, degenerate mineral mess used by farmers and horticulturalists to grow plants - may contain plenty of nutrients, but it is far from improved. It is structurally, chemically and ecologically depauperate, useless unless continually given the treatment that first damaged it. Most natural soils are far from infertile. They function perfectly well by recycling relatively small quantities of nutrients *via* their own biological components. In fact they cannot function properly if over fertile. They just seem to us to be infertile because we are stuck with the idea that, in order to grow plants, tillage and input are mandatory. Modern agriculture succeeds in producing food, but at what cost? (Harvey 2001).

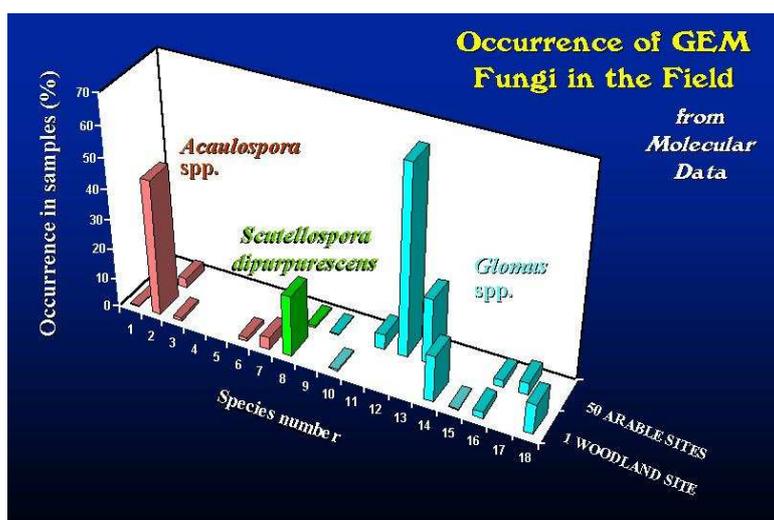


Figure 4 Chart illustrating differences in the glomalean endomycorrhizal populations at a single woodland site and the combined data from fifty arable field sites (wheat and peas). Note that the arable sites were dominated by two closely related species of *Glomus* (other taxa occurred sporadically), whereas at the woodland site there is a wide diversity of GEM fungi (11 species in four genera to date). Data from molecular studies carried out by members of the University of York mycorrhiza research team.

Research at the University of York has shown that the community of mycorrhizal fungi in arable soils is highly modified from that found in the woodland that might once have occupied the same site (Helgason *et al.* 1998). A few species of glomalean fungi that are tolerant of tillage and high input are dominant in arable soils, and they will associate promiscuously with most plants, often with little host benefit. In contrast, the mycorrhizal fungal community in woodland is much

more diverse and the arable soil fungi are absent or, if present, they do not dominate (Figure 4). Also some plants and fungi show a degree of partnership selectivity (Molina & Trappe 1982; Merryweather *et al.* unpublished). Some fungi can contribute to plant functioning only as an intact 3-dimensional mycelium; they are very easily upset by tillage and can be very particular about which host they choose. Even the most aggressive root colonisers might have a favourite host or hosts at certain times of the year.

If a plant species is removed from a community, some of the fungi with which it naturally interacts, and which it supports, will disappear (Figure 3). If many or all plants are removed, then the natural mycorrhizal community will be severely reduced or even wiped out. If land is then subjected to agricultural abuse, the effect on the soil community will be to change it into something entirely unlike that which supported the lost natural community: paradoxically, enriched but impoverished. Imagine the consequences of keeping exhausted land 'fallow', as is recent practice, with the plough or herbicides.

Habitat restoration: a hopeless cause?

These days, the starting point for habitat restoration is more often than not abandoned arable or polluted industrial land. Consider also current valiant attempts to reforest Scottish upland, devoid of trees and dominated by plants that have supported the wrong mycorrhizal fungi for the past several thousand years, e.g. heathers (ericoid endomycorrhizal), moorland grasses (GEM) and rushes (non-mycorrhizal). Many important woodland trees are ectomycorrhizal. Planting trees in degraded, or at best modified, soils with the hope of creating woodland has to be thoroughly unrealistic and the evidence can now be seen everywhere in Britain: millions of empty plastic tree tubes.

The trees we associate with proper ancient woodland are not high on the easy-to-grow list, and some or many individuals will simply fail to survive. Others, which are less dependent upon mycorrhiza, or are less particular about the fungi with which they associate, may do better. Do Ash, Cherry, Alder, Willow and Sycamore sound familiar in this context? (Table 1). But woodland is much more than a plantation of unsuitable trees, although I suspect many folk (probably not BW readers) would be content with straight rows of sickly, weed-choked trees within which to void the dog. Woodland as we understand it - the pity is, and this is very important, we don't - would take hundreds, maybe thousands of years to develop where a farmer's crops used to grow.

This is plainly illustrated by the Geescroft Wilderness experiment on the Broadbalk plot at Rothamsted, abandoned to natural processes in 1882. What has replaced wheat and field beans after 120 years consists of: "...mainly ash and sycamore, with a hawthorn understorey and ground ivy in the middle...and mature deciduous woodland dominated by oak and ash with a rapidly expanding understorey of holly leading to otherwise poor ground cover", nothing like fully developed woodland. Modern arable soils are more severely modified and likely to be even less able to support the development of a proper wild community.

If it is required, as it should be, a woodland ground flora that is also dependent upon the soil community will not develop. Certainly, seed can be sown or plants planted. I have seen the results of such projects and it is the pioneer, non-mycorrhizal (Red Campion, Greater Stitchwort), less mycorrhiza dependent (Primrose) and symbiotically promiscuous species (Bugle) that flourish, whilst many familiar favourites and less attractive woodland plants fail or are not even considered for planting because they are known to be difficult (Bluebell, Yellow Archangel, Wood Anemone etc. Table 1). I do not denigrate the efforts of those charged with rectifying environmental damage already perpetrated. At Milton Keynes, where anything is an improvement on the 1960s trees and weeds or bare ground, ecological miracles are being performed, but classic ancient woodland is still a long way off (Francis & Morton 2001).

Well, why not just add mycorrhiza?

If mycorrhiza is so important, why not just 'add it' when planting? Wouldn't that be a wonderful remedy? Mycorrhizologists wryly refer to the idea as 'The Golden Bullet', which at the moment it is only a dream; a dream that is making a number of hasty

entrepreneurs a living and many of their customers disappointed. Still, we need to chase that dream if we are to recover a decent countryside from its ragged remnants.

Anybody can produce industrial quantities of mycorrhizal material using both ecto- and glomalean endomycorrhizal fungi, but only of those species which are amenable to cultivation. If inoculant manufacturers care to provide a list of ingredients - most try to keep such things secret - it can be seen that their constituent fungi are those that are easy to grow: *Pisolithus tinctorius*, *Rhizopogon* spp., *Glomus mosseae*, *G. intraradices*, *G. monosporum* and *Gigaspora margarita*, not those that might be ecologically relevant, for example *Scutellospora dipurpureascens*, *Glomus hoi*, *Archaeospora trappei* and numerous unidentified and un-named fungi we find in the wild (11 with Bluebell alone at a single Yorkshire site). Incorporation of such cocktails, if they are in good condition, might give an individual young tree advantage over others, make your lawn greener or potted glasshouse strawberries grow better. They do not contain fungi that matter in real situations, and there is little to guarantee that the constituents of a commercial inoculant will be viable or usefully active in every, if any, particular ecological application. Soil decompaction and T.L.C. might restore the vigour of a sickly mature tree, but 'magic mycorrhiza dust' placed around its roots will not. If a tree is not mycorrhizal, it is a dead tree!

We might care to ponder the fact that some of the fungi in commercial inoculants are probably not native to the U.K. (e.g. the entire genus *Gigaspora*) yet there are no laws to prevent foreign glomalean fungi being introduced into our alien saturated countryside.

A wild community such as woodland is a diverse collection of plants plus all the other organisms which go to make a natural ecosystem. We barely know what the constituent organisms are, let alone how they all interact, and that includes the mycorrhizal fungi and the plants with which they associate. The addition of handfuls of easy-culture fungi to any plant or group of plants has to be a naïve expedient; that is, until we have developed sufficient knowledge and skill to culture and intelligently manipulate the fungi that matter to Bluebell, Wood Anemone, Wavy Hair-grass, Oak and Elm to the benefit of them and all the other wild plants.

This branch of ecology is in its infancy and research effort limited. Let us hope that it does not take too long, because we need to be able to exploit mycorrhiza right now. Apparently, we now have genetically modified, Dutch Elm Disease resistant Elms. That's terrific, but where should we site them in a landscape that has changed since Elm was exterminated? How shall we grow them? They will be grown in nurseries and then planted out by digging holes and bunging them in - in tubes. I could be wrong, but I suspect that that growth will be erratic and many will fail to reach maturity. I wish we had the knowledge to advise growers how it should be done.

The present state of affairs puts one in mind of Gerald Durrell's gloomy observation:

"It's as though life had given us a delicately adjusted clock to tell us the time for ever, and without knowing how the hell it works, we at once open up the back and start fiddling around with a blunt screwdriver".

Leave well alone

Would we demolish York Minster to make way for a by-pass, confident that, without detailed records of everything that went to make up the original during the past 1,000

years, we could build an exact replica at a more convenient site using reinforced concrete, steel girders and recycled plastics, referring from time to time to the architecture of an assortment of tumbledown parish churches?

Why, then, do we permit the continued destruction of the last remnants of our countryside to satisfy the greed of modern life, ignorant of what it is we are destroying and, consequently, of how to rebuild it? Anyone can see that the controversial Newbury bypass occupies an area hugely less than the ancient woodland callously sacrificed to create it, and that the many hectares of damaged land to either side of the new road have been artificially planted with replacement 'woodland'. Apparently we are content to see the land infested with plantations of plastic tubes; dead, moribund or inappropriate trees and rank weeds, with little hope of enjoying what, before the war, we were able to take for granted (Harvey 2001).

It is ludicrous for any organisation bent on 'development' of a precious piece of countryside to promise that planting thousands of trees somewhere else (some claim millions in their PR publications) and some expensive landscaping can compensate for the destruction of a wild site. No ecosystem can recover from the brutal treatment man is capable of dishing out with today's machinery except it is allowed the sort of time it took for our islands to recover from devastation wrought by the Devensian glaciers! Then, there was a diverse reservoir of species remaining to enable recolonisation of the north, very unlike large parts of our miserable, degenerate landscape with its few isolated islands of natural worth.

It is also ludicrous to think that a high quality wood, meadow or salt marsh can be scraped up in chunks and redeposited in a more convenient place. If only the 3-D structure and ecological role of the single factor under discussion here - mycorrhiza - were to be considered, the lethal effect of mechanical stress upon millions of miles of crucial mycelium attached to the plants which would be expected to continue growing after transfer would be an obvious reason not to attempt it.

The ecologies of mycorrhiza and the other communities of soil organisms are infinitely (probably literally) more complex than we can possibly understand today. Nevertheless, belowground processes must play a part in ecological thought when the exploitation and conservation of the countryside are under consideration or we will continue to make appalling mistakes. The best way to have British woodland, tropical rain forest or any other wild community to enjoy is to leave it alone and keep it as it always was. Where it has already been lost, of course we must make desperate repairs, but we must not deceive ourselves: we do not know how it can be done and we will never see full recovery in our lifetime.

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Table 1 The mycorrhizal status of common British woodland trees and understorey plants. EcM = ectomycorrhizal; GEM = glomalean endomycorrhizal; N-M = non-mycorrhizal or nearly so. Data extracted mostly from Harley, J L & Harley, E L, 1987 A check-list of mycorrhiza in the British flora. *New Phytologist* Suppl. 105: 1-102 and updates, 1987 and 1990.

Botanical name	Common name	Mycorrhizal status
Trees		
<i>Castanea sativa</i>	Chestnut	EcM
<i>Corylus avellana</i>	Hazel	EcM

<i>Fagus sylvatica</i>	Beech	EcM
<i>Fraxinus excelsior</i>	Ash	EcM
<i>Larix decidua</i>	Larch	EcM
<i>Pinus sylvestris</i>	Pine	EcM
<i>Quercus</i> spp.	Oak	EcM
<i>Salix</i> spp.	Willow	EcM
<i>Acer pseudoplatanus</i>	Sycamore	GEM
<i>Aesculus hippocastanum</i>	Horse Chestnut	GEM
<i>Crataegus monogyna</i>	Hawthorn	GEM
<i>Ilex europaeus</i>	Holly	GEM
<i>Prunus</i> spp.	Cherry	GEM
<i>Salix</i> spp.	Willow	GEM
<i>Sorbus aucuparia</i>	Rowan	GEM
<i>Taxus baccata</i>	Yew	GEM
<i>Ulmus</i> spp.	Elm	GEM
none	none	N-M
Understorey plants		
none	none	EcM
<i>Ajuga reptans</i>	bugle	GEM
<i>Allium ursinum</i>	ramsons	GEM
<i>Anemone nemorosa</i>	wood anemone	GEM
<i>Circaea lutetiana</i>	enchanter's nightshade	GEM
<i>Galanthus nivalis</i>	snowdrop	GEM
<i>Galeobdolon luteum</i>	yellow archangel	GEM
<i>Glechoma hederacea</i>	ground ivy	GEM
<i>Holcus mollis</i>	wavy hair-grass	GEM
<i>Hyacinthoides non-scripta</i>	bluebell	GEM
<i>Lysimachia nummularia</i>	creeping jenny	GEM
<i>Mercurialis perennis</i>	dog's mercury	GEM
<i>Narcissus pseudonarcissus</i>	wild daffodil	GEM
<i>Oxalis acetosella</i>	wood sorrel	GEM
<i>Poa trivialis</i>	rough meadow grass	GEM
<i>Primula vulgaris</i>	primrose	GEM
<i>Prunella vulgaris</i>	self heal	GEM
<i>Pteridium aquilinum</i>	bracken	GEM
<i>Rubus fruticosus</i> agg.	bramble	GEM
<i>Teucrium scorodonia</i>	wood sage	GEM
<i>Viola riviniana</i>	common violet	GEM
<i>Silene dioica</i>	red campion	N-M
<i>Carex</i> spp.	sedges	N-M
<i>Stellaria holostea</i>	greater stitchwort	N-M