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Towards a functional classification of ectomycorrhizal fungi

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Abstract. Ectomycorrhizal (ECM) fungi have previously been divided into two groups ('early-stage' and 'late-stage') based on their position in 'ectomycorrhizal succession'. This classification has a number of limitations, particularly in the lack of precision in the terminology adopted and its general applicability. Many species cannot be easily assigned to either stage, and the behaviour of some species is modified by environmental conditions. In addition, a number of different mechanisms of ECM succession have been proposed, including the influence of organic matter and root exudates. In this paper, it is suggested that the phenomenon of ECM succession can be explained simply by the relative ability of different fungi to colonize and spread from different sources of inoculum. Epidemiological characteristics, such as the ability to produce mycelial strands or to spread on root systems by secondary infection, may therefore provide a more appropriate basis for a functional classification of ECM fungi. The functionally important characteristics of ECM fungi are discussed.

Key words: Ectomycorrhizas – Mycorrhizal succession – Classification

Introduction

The classification of species into groups based on functional characteristics reveals overall patterns and facilitates the production of generalizations and predictions about ecological processes. Progress has been made in the development of such classifications for higher plants (Grime 1985; Swaine and Whitmore 1988). However, only partial progress has been made towards such a system of classification for ectomycorrhizal (ECM) fungi, despite the importance of these organisms for ecological processes in many temperate and tropical forest communities (Allen 1991).

ECM fungi have previously been divided into two categories, 'early-stage' and 'late-stage', based on the temporal pattern of basidiocarp appearance following tree establishment (Mason et al. 1982, 1983). I believe that this classification has a number of limitations, both in the terminology adopted and in its general applicability. In this paper, I propose that an alternative classification may be developed, based on the functional characteristics of ECM fungi. Recognition of a larger number of functional types should result in a greater awareness of the diversity in patterns of behaviour of ECM fungi encountered in natural ecosystems.

Early-stage and late-stage classification

Two groups of ECM fungi were identified by Mason et al. (1982, 1983) on the basis of the temporal and spatial patterns of basidiocarp production around *Betula* trees established on agricultural soils. Species of *Inocybe*, *Hebeloma*, *Laccaria* and *Thelephora*, which appeared within the first 4 years after planting, were followed largely in later years by species of *Lactarius*, *Leccinum*, *Cortinarius* and *Russula* (Mason et al. 1982). These two groups of species were termed 'early-' and 'late-stage', respectively, according to their position in the 'mycorrhizal succession'.

The relationship between the occurrence of basidiocarps and mycorrhizas was investigated by Deacon et al. (1983), who found increasing numbers of *Hebeloma* mycorrhizas and decreasing numbers of *Leccinum* mycorrhizas with increasing distance from the tree. When mycelial inocula were added to natural soils, or when seedlings were grown in soil cores collected from beneath basidiocarps of different fungi, only early-stage fungi were able to infect seedling roots (Deacon et al. 1983). In an additional series of experiments with a wide variety of species, Fox (1983, 1986) found that only early-stage genera (such as *Inocybe*, *Hebeloma* and *Laccaria*) were able to infect seedlings from spore inocula added to mineral soils.

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The dichotomous classification of ECM fungi based on their pattern of appearance in mycorrhizal succession has a number of limitations. Firstly, as the original observations were made of trees established on an agricultural soil, the results arguably have little relevance to forested sites. This is highlighted by the results of Fleming (1983a, 1984), Fleming et al. (1986) and Newton (1991), who found that seedlings established near mature trees on forest soils became infected predominantly by late-stage types. The fact that mycorrhizal succession seems to be 'bypassed' in such circumstances is noted by Mason et al. (1987). These results indicate that the terminology used to describe the two groups of fungi is inappropriate (Fleming 1983b), as late-stage fungi are able to colonize seedling roots if the appropriate inoculum is available.

An additional problem with this terminology is the difficulty in defining a 'stage'. Arnolds (1991) has pointed out that the terminology is misleading, because the term 'late-stage' suggests optimal occurrence in late-successional stages, often considered to be 40 or more years old. In fact, many late-stage species may be abundant in stands 5–10 years old (Arnolds 1991), as recorded in the original descriptions of succession (Mason et al. 1982, 1983). In addition, early-stage fungi are by no means restricted to seedlings or young trees, and are regularly found in association with mature trees in plantations or semi-natural forests (Malacjzuk 1987; Danielson and Pruden 1989; Arnolds 1991; A. C. Newton, unpublished observations).

The general applicability of the early- versus late-stage classification is also limited by the influence of soil type on the behaviour of ECM fungi (Last et al. 1985; Fleming et al. 1986; Mason et al. 1986). For example, *Paxillus involutus* was able to infect *Betula* from spore inocula to a far greater extent on coal spoil than brown-earth soil (Fox 1986). This is consistent with the fact that *Paxillus*, *Scleroderma* and *Pisolithus* spp. are more characteristically the primary colonizers of coal spoil and other mining waste (Marx 1980; Gardner and Malajczuk 1988; Ingleby et al. 1985). However, *P. involutus* and *Scleroderma citrinum* may be equally dominant in mature (>50-year-old) plantations established on sandy soils (Newton 1989, 1991).

The problems outlined above have led to confusion in the application of this classification to different species. For example, although *Cortinarius* spp., *Lactarius* spp. and members of the *Boletaceae* are generally considered to be late-stage fungi (Dighton and Mason 1985), a number of species of these genera were described as early-stage by Arnolds (1991) on the basis of their association with relatively young trees. *Lactarius pubescens* apparently possesses characteristics of both early- and late-stage fungi and has consequently been classified as 'intermediate' (Fleming 1983a, 1985; Fleming et al. 1986; Gibson and Deacon 1988).

Mechanisms of mycorrhizal succession

A number of mechanisms have been proposed as the basis of the difference between early- and late-stage fungi. Last et al. (1983, 1985) suggested that the key difference is related to the response of the different fungi to other soil microbes during infection. Dighton and Mason (1985) proposed that the carbohydrate requirement of the fungus is crucial, early-stage fungi having a lower carbohydrate requirement for rapid growth in culture. Last et al. (1987) attributed the observed differences to the relative abilities of different species to colonize roots in the presence of different types of litter. Gibson and Deacon (1988) suggested that ECM fungi differ in their ability to infect root tips depending upon the age of the root as a result of a change in the carbohydrate supply with root development.

The main difference between early- and late-stage ECM fungi is their ability to colonize root systems from different sources of inoculum, early-stage species being more able to colonize from spores and small amounts of mycelial inocula in pot culture or soil cores (Deacon et al. 1983). However, Fleming et al. (1986) demonstrated that late-stage genera such as *Cortinarius*, *Lactarius*, *Leccinum* and *Tricholoma* spp. were able to colonize seedlings when grown in pots of soil from a forested site. Similar results were obtained by Newton (1991), who found that many of the ECM types that infected seedlings grown on forest soils were able to infect both in pots and in the field. These latter results indicate that late-stage fungi can infect from small amounts of inoculum or isolated inoculum if an attempt is made to limit disturbance to the soil during sampling.

The results of Fleming et al. (1986) have been attributed to the difference in soil conditions between agricultural and forest sites and the role of organic matter in particular. For example, Last et al. (1987) proposed that late-stage fungi require accumulations of recalcitrant leaf litter in the soil in order to colonize tree roots successfully. Similarly, Dighton and Mason (1985) considered that the increasing recalcitrance of forest floor organic matter during forest development may influence the development of ECM communities. Many early-stage fungi are certainly characteristic of mineral soils (Danielson 1985), and this has supported the view that litter accumulation is a driving force in mycorrhizal succession (Gardner and Malacjzuk 1988). However, some early-stage species are able to colonize highly organic substrates (Last et al. 1985; Dighton et al. 1986).

In fact, the influence of organic matter on the growth and activity of ECM fungi is poorly defined. After soil disturbance, ECM inoculum may be restricted to pockets of soil rich in organic matter (Christy et al. 1982; McAfee and Fortin 1989), perhaps reflecting the requirement for organic material as a nutrition source (Dighton and Mason 1985). Alternatively, there is evidence that the accumulation of recalcitrant substances in litter may inhibit basidiocarp production (Jansen and van Dobben 1987; Kuyper 1988). There are few experimental data to support the view that organic matter is important in ECM succession; most of the evidence is based on correlation. When organic amendments were added to mineral soils, Danielson (1991) found no effect on ECM succession.

I believe that ECM succession can be understood solely in terms of the build-up of inoculum following tree establishment. When a tree becomes established on a previously unforested site, the ECM inoculum available will primarily be in the form of spores. Those fungi particularly able to colonize from spore inocula (early-stage fungi) will tend to colonize first. However, most species of ECM fungus of forest systems depend on mycelial inocula for infection (Mason et al. 1987). Mycelial infection depends upon the build-up of inoculum on the root systems of the plant and on the spread of secondary infections (Chilvers and Gust 1982). Those species that are able to generate high inoculum potentials by the build-up of mycelial inoculum on root systems will tend to predominate with time.

The fact that early- and late-stage ECM fungi differ in the inoculum potential required for infection has been noted previously (Deacon et al. 1983; Fleming 1985; Gibson and Deacon 1988). Similarly, the replacement of species that establish primarily from spores by those that colonize primarily from mycelial inocula has been recognised as a feature of ECM succession (Mason et al. 1987). However, I suggest that the importance of this process has been underestimated in the past. The phenomenon of ECM succession can be attributed solely to the relative ability to colonize and spread from different sources of inoculum; no other mechanism need be invoked.

The basis of an alternative classification

The prevailing environmental conditions, together with the availability of different sources of inoculum, will influence which fungi are able to grow and colonize any particular site, but the outcome of competitive interactions between ECM fungal species will be determined primarily by their ability to colonize and spread on the root systems of host species from different sources of inoculum. I suggest that the epidemiological characteristics of ECM fungi which determine competitive ability (cf. Parke 1985) should form the basis of any functional classification.

The association of a small group of ECM fungi, including *Hebeloma*, *Inocybe*, *Laccaria* and *Thelephora* species, with young trees grown in pots or nurseries, or when colonizing previously unforested sites, has in fact been recognized for some time (Trappe and Strand 1969; Marx et al. 1970; Mikola 1973; Trappe 1977; Chu-Chou 1979). I attribute the abundance of these species in such circumstances to their well-documented ability to establish from spore inocula or sources of low inoculum potential (Fox 1986). As described earlier, the epithet 'early-stage' is both misleading and inaccurate. I therefore suggest that the term 'pioneer' fungi should be more widely adopted. This term is already present in the literature (Watling 1981; Mason et al. 1987; Arnolds 1991) and is also applied to higher plants with analogous patterns of behaviour (Grubb 1987; Swaine and Whitmore 1988).

Whilst the group of pioneer fungi is relatively well defined, this leaves thousands of ECM species which occur globally (Trappe 1962; Malloch et al. 1980) classified together in a single category (late-stage). It is this lack of appreciation of the diversity of ECM fungi to be found in forested ecosystems which is the least satisfying aspect of the current dichotomous classification. Arnolds (1991) proposed that, apart from pioneer fungi, 'early-', 'intermediate-' and 'late-successional' species might also be differentiated. Although I agree that such groups subsequently may be defined, the aim here is to highlight the variation in the ECM fungi which exist in natural systems, and to suggest those functional characteristics that may form the basis of a future classification.

As noted above, I believe that epidemiological characteristics may provide a suitable set of criteria by which ECM fungi may be grouped. As ECM colonization in forests is primarily by mycelial inocula, the behaviour of this mycelium and its structure may be considered to be of relevance. Mycelial strands have been identified as of particular importance as a source of inoculum, as well as a transport mechanism for water and mineral nutrients (Skinner and Bowen 1974; Marx 1980; Fleming 1984; Read et al. 1985). Not all ECM species produce mycelial strands (Bowen 1973) and, perhaps significantly, neither do many pioneer fungi (Mason et al. 1987). Species such as *Paxillus*, *Scleroderma* and *Pisolithus* are also prolific strand formers, which may account for their ability to persist on sites adverse to hyphal growth, such as coal spoil and mine waste (Marx 1980; Newton 1991). *Paxillus involutus* and *S. citrinum* are also able to spread rapidly and dominate root systems in sandy soils (Newton 1991; Newton and Pigott 1991).

The build-up of ECM infection on root systems, which may act as a source of inoculum for secondary infection, is also influenced by the ability of the mycorrhizas to branch and form 'clusters' of infection (Chilvers and Gust 1982). Branching ability is obviously influenced by the state of development of the mycorrhiza and in some cases by the host species involved (Zak 1973). However, branching ability does seem to be consistent for some ECM fungi, e.g. *Cenococcum geophilum*, which is always unbranched (Pigott 1982). Coincidentally, this species is often low in abundance when other ECM fungi are present, and is not characterized by a marked ability to spread rapidly on root systems (Newton and Pigott 1991).

The spread of secondary infection by mycelia is also influenced by the availability of uninfected root tips (Chilvers and Gust 1982). In this way, a higher rooting density provides a higher number of sites available for colonization and must favour those fungi that spread by mycelial inocula. This may partly account for the later appearance of late-successional fungi following tree establishment and for their association with the older parts of root systems. Gibson and Deacon (1988) demonstrated that *Lactarius pubescens* (a strand former) preferentially infected older regions of the root system when mycelial inocula were added to the soil. These results were interpreted to indicate the importance of root age in determining infection. In fact, the higher rooting density in the older parts of the root system may have contributed to the build-up of infection. The fact that *L. pubescens* is able to infect young (seedling) roots was illustrated by their own experiments; seedlings established close to sources of high inoculum potential near the roots of an older tree became infected (Gibson and Deacon 1988).

The ability of a fungus to colonize and spread on a root system will also be affected by the prevailing environmental conditions, because ECM fungi display a variety of responses to climatic and edaphic factors at both the inter- and intraspecific levels (Brundrett 1991). The host species involved must also influence the spread of infection, if only because mycelial growth depends upon the carbon supply from the host. Many ECM fungi display patterns of preference or specificity for different host species, such that the extent of infection (or even the degree of branching of the mycorrhizas) depends upon the host species infected (Molina and Trappe 1982; Newton 1991). Classifications of species based upon the breadth of their preferred host range are of value in highlighting the variation in behaviour of ECM fungi in natural systems (Molina and Trappe 1982). The functional basis of host preference may not necessarily be found in ultrastructural analysis of the host-symbiont interface, but through an increased understanding of the factors that determine the rate of carbon transfer to different ECM symbionts.

In terms of the host plant, two other attributes of the ECM fungus are of functional importance: the effectiveness of nutrient capture, and the efficiency of nutrient transfer to the host. These aspects depend at least partly upon the extent and activity of the external mycelium. In this context, the results described by Abuzinadah and Read (1986) are of relevance. *Hebeloma crustuliniforme*, *Paxillus involutus* and *Amanita muscaria* displayed a similar ability to degrade protein in culture, but the species differed in their ability to transfer N and promote the growth of the host; the pioneer species (*H. crustuliniforme*) outperformed the other two symbionts.

In conclusion, I believe that progress can be made towards defining functional groupings of ECM fungi based on the criteria outlined above. Few data are available concerning the functional characteristics of different ECM symbioses, and more comparative experiments, such as those described by Abuzinadah and Read (1986), are required if more precise classifications are to be developed.

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