

1 Towards Ecological Relevance – Progress and Pitfalls in the Path Towards an Understanding of Mycorrhizal Functions in Nature

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1.1 Summary

The major achievement of the first hundred years of research on the mycorrhizal symbiosis is the observation that the symbiosis is almost universally present in natural communities of terrestrial plants. However, studies of the functional characteristics of the mycorrhizal associations used, for the most part, reductionist approaches, and the role of the symbiosis in the dynamics of terrestrial plant communities was largely overlooked. This chapter, along with others contained in the book, describes attempts made so far to place the mycorrhizal function in the broader context. The strengths and weaknesses of reductionist approaches to investigation of mycorrhizal function are assessed and the overriding need to recognise and tackle the inherent complexity of plant and microbial communities is seen as a fundamental prerequisite for progress towards ecological relevance. Two distinct pathways are seen to have the potential to facilitate this progress, one involving ‘microcosm’, the other ‘field’ approaches. The relative advantages and disadvantages of each approach is examined and the features of experimental design which will enhance the potential to obtain ecologically meaningful outputs are consid-

ered in detail. It is concluded that, in addition to the requirement for greater sophistication in our experimental approaches, there is a need for more effective collaboration with specialists in related disciplines, most notably soil chemists, bacteriologists, micro-faunists and those dealing with other fungal groups, if we are to gain an appreciation of the status of the mycorrhizal symbiosis in the larger context of ecosystem function.

1.2 Introduction

It is heartening as we enter the second century of research on mycorrhiza that attention is increasingly focused on the functions of the symbiosis in the natural and semi-natural systems in which it evolved. This volume, while encapsulating the spirit of the new adventure, also provides two further opportunities. It enables us to assess the strength of the platform from which we launch into this challenging area and to identify which experimental approaches might provide the most realistic evaluation of the roles played by mycorrhizae in natural communities.

1.3 The Platform Provided by Reductionist Approaches

It can justifiably be claimed that a major achievement of the first hundred years of research on the mycorrhizal symbiosis was to force recognition, amongst an initially largely sceptical scientific community, that the symbiosis was almost universally present in natural communities of terrestrial plants. Over this period, much emphasis has been placed on activities of the cataloguing kind. Six major types of mycorrhiza have been recognised (Harley 1959; Harley and Smith 1983; Smith and Read 1997; Read 1998), so that the basic structural and functional attributes of each can be summarised (Fig. 1.1). The taxonomic position of the fungi forming these types is understood, at least in broad terms, and the pattern of their distribution amongst plant families (Trappe 1987) and species (Harley and Harley 1987) is known.

Recently, the application of molecular methods to analysis of the taxonomic and phylogenetic relationships within the major groups of mycorrhizal fungi (e.g. White et al. 1990; Simon et al. 1992) has yielded valuable new insights. For instance, exciting discoveries have been made to describe host specificity and coevolution between plants and mycorrhizal fungi based on molecular methods (Taylor et al., Chap. 15, this Vol.). These approaches also promise to reveal much about mycorrhizal community structure in the field (Clapp et al., Chap. 8, this Vol.). Unfortunately, progress towards understanding how mycorrhizae influenced the functions of plant and microbial com-

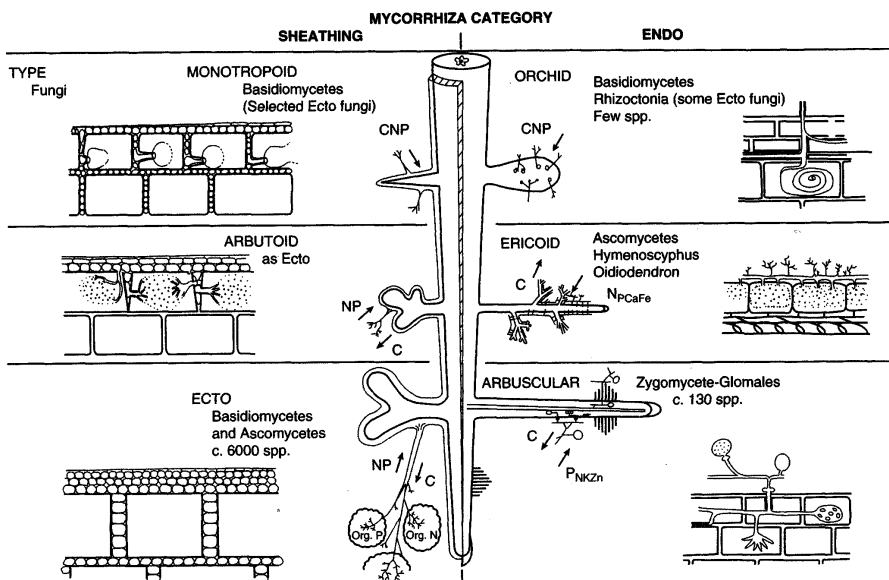


Fig. 1.1. The diagnostic structural features of the six recognised types of mycorrhiza. Two basic categories are designated, one in which the root surface is sheathed in a fungal mantle (*SHEATHING*), and one lacking a mantle but in which hyphae proliferate internally (*ENDO*). The defining structures of each type are fungal pegs (*MONOTROPOID*), Hartig net and intracellular penetration (*ARBUTOID* – also seen in the subtype ‘ectendo’), Hartig net, mantle, external mycelial network (*ECTO*), peloton (*ORCHID*), hyphal complexes in hair roots (*ERICOID*) and arbuscules or hyphal coils (*ARBUSCULAR*). The most important nutrient acquisition pathways are shown. C Carbon, N nitrogen, P phosphorus, Org organic, K potassium, Zn zinc, Ca calcium, Fe iron. Predominant directions of flux of each element are indicated by arrows. (Modified from Read 1998)

munities in nature has no match to that achieved in the descriptive areas. There have been serious attempts, largely based on extrapolation of results obtained in laboratory studies, to suggest what these functions might be in ecosystems but they consist, in essence, of hypothetical scenarios that remain to be tested (see e.g. Allen 1991; Read 1991). We find ourselves in this unsatisfactory situation largely because, faced with the complexity of natural systems, the response of many experimentalists was to adopt reductionist approaches. Experimental designs were simplified to the extent that their ecological relevance was compromised. We now require an evaluation of the extent to which those approaches have provided insights into mycorrhizal function in the real world

Some useful insights have undoubtedly been gained. Thus, the sheer number of experiments carried out under ‘controlled’ conditions enable us to make firm predictions about the processes whereby nutrient supplies to individual roots, as well as to single plants, usually grown for short periods of time in small containers, are augmented. Details about nutrient uptake and supply

by ecto-mycorrhizal fungi (EMF) and arbuscular mycorrhizal fungi (AMF) are given by Simard et al. (Chap. 2, this Vol.) and Jakobsen et al. (Chap. 3, this Vol.) respectively. However, the results produced by such experiments describe only the potential of the symbiosis. We remain largely ignorant of the extent to which this potential is expressed in nature. Insofar as excision of the root removes the major vegetative components of both the plant and fungal partners, while containerisation of individual plants or species removes interactions between them, neither approach can provide a platform from which to establish a meaningful assault upon questions of function at the ecosystem level.

Reductionism has afflicted mycorrhizal research in other ways. Not only has there been an overemphasis upon studies of the nutritional role of the symbiosis but also a preoccupation with its involvement in phosphorus (P) supply to the plant. At its height, this enabled review articles describing nutrient supply and demand to mycorrhizal plants to deal exclusively with the phosphate ion (see, for example, Koide 1991). One consequence of these pre-occupations is that mycorrhizae have become defined as 'symbioses in which an external mycelium of a fungus supplies soil-derived nutrients to a plant' (Smith and Read 1997). While not being necessarily inaccurate, such definitions carry with them the implication that absorption is the key, if not the only, function of the symbiosis. A broader view emphasising evolutionary perspectives, recognises that gene transfer is the key driver in natural selection and considers the symbiosis in terms of its contribution to the reproductive success or 'fitness' of the partners. Viewed in this way, a mycorrhiza is more appropriately defined as 'a structure in which a symbiotic union between a fungus and the absorbing organs of a plant confers increases of fitness on one or both partners' (Read 1999). This definition is compatible with the emerging recognition of the multifunctional nature of the symbiosis (Newsham et al. 1995a).

At the community level we are aware that mycorrhizae may express a number of potential attributes both of nutritional and broader kinds. Amongst those perceived to be of likely importance to the plant partner are the abilities to mobilise a range of nutrients from complex substrates (Aerts, Chap. 5 and Leake et al., Chap. 14, this Vol.), the provision of resistance to disease (Carey et al. 1992), to the effects of naturally occurring climatic stresses like drought (Allen and Allen 1986) and to the impacts of pollutants (Meharg and Cairney 2000). At the same time AMF and most EMF appear to be obligately dependent upon their autotrophic associates for the resources necessary to produce reproductive propagules. The result of this broader perception of the nature of the mycorrhizal condition is, that its importance for both plant and fungus is recognised to go beyond that of absorption to make wider contributions to survival, fecundity and hence 'fitness' of the partners (Read 1997, 1999).

Greater awareness of these more fundamental biological attributes of the symbiosis is timely because it should enable them to be considered when

ecosystem scale experiments are being designed and analysed. It leads to an emphasis on the need to examine responsiveness of the mycorrhizal partners over their full life cycles or at least over critical parts thereof, in the presence of the environmental variables likely to be imposed upon the systems in nature. Since these variables themselves differ at global (e.g. latitudinal) and local (e.g. edaphic) scales, it can be predicted that selection will have favoured distinctive attributes in the plant and fungal partners under each environmental circumstance. These attributes have been readily recognised by plant ecologists and used to define biomes (Odum 1971) or communities (Ellenberg 1988) based upon suites of largely phenological characteristics seen above ground.

That similar selective forces have moulded mycorrhizal fungal communities is indicated by the changes observed at the global scale in the extent of occurrence of arbuscular mycorrhizal, ecto-mycorrhizal and ericoid mycorrhizal categories of the symbiosis in different biomes (Read 1991). While these shifts are relatively easy to detect, there is every likelihood that effects at the more local scales will influence selection of genotypes within each category of the symbiosis but, to date, we have been less aware of this possibility. Small scale changes of community structure, for example of the kind enabling identification of particular phyto-sociological units within broader groupings, *sensu* Braun-Blanquet (1928) and Rodwell (1991), may well be linked to, even driven by, distinctive genotypes of mycorrhizal fungi. The recent demonstration (van der Heijden et al. 1998a,b) that genotypic diversity within AM fungal communities can have major impacts upon the performance and compo-

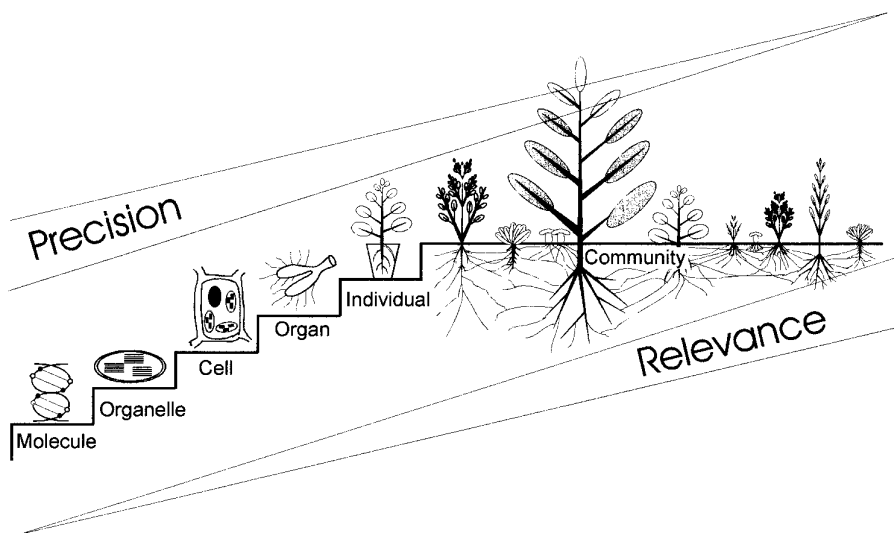


Fig. 1.2. Studies of the mycorrhizal symbiosis can be carried out at a number of levels. As we move up the hierarchy of complexity there is a likelihood that our observations have greater relevance but at the expense of precision. (Modified from Körner 1993)

sition of plant assemblages is strongly suggestive of such effects (for further information see Hart and Klironomos, Chap. 9 and van der Heijden, Chap. 10, this Vol.). Clearly, such observations are of direct relevance to issues of conservation and biodiversity below and above ground which are in urgent need of further investigation.

The 'retreat' from the challenge posed by complexity is not a unique feature of mycorrhizal research. The problems posed by the need to scale up from readily tractable simple questions to the multifactorial issues that determine ecosystem function have been acknowledged by ecologists (e.g. O'Neill et al. 1986). Körner (1993) recognised a hierarchy of complexities along which, as studies advance from the molecular, cellular or organ levels to those at the community scale, precision was inevitably lost, the great compensation being that gains in ecological relevance were obtained (Fig. 1.2). In the context of mycorrhizal research, the 'wood-wide web' of symbiotic mycelium which forms a network connecting individual species, genera, even families of plants in natural communities (Simard et al., Chap. 2, this Vol.; Read 1997) provides a good example of the complexity which prevails in the upper echelons of the hierarchy, but which is inevitably overlooked by reductionist approaches. The need to recognise such complexity and to incorporate it into experimental design will be emphasised through the remainder of the present chapter and throughout this book.

1.4 Approaches to Examination of Mycorrhizal Function at the Community Level

It is evident from Fig. 1.2 that as we advance to ask questions about the role of mycorrhiza in ecosystem processes, the complexity required of our experimental designs will, of necessity, become progressively greater. Some, the reductionists, would say that they become so great as to render the questions unanswerable but such counsels of despair may derive as much from fear of the logistics of ecosystem scale experiments as from problems inherent in the science itself. Those who latterly have ventured into the new and challenging domain have done so by two different routes which can be designated 'microcosmic' (Sect. 1.4.1 sensu Grime et al. 1987; van der Heijden et al. 1998a,b) and 'field' (Sect. 1.4.2 sensu Fitter 1986). These mirror approaches, also only recently developed, taken by ecologists to investigate the 'rules of association' in plant communities assimilating the information gained from both approaches to produce broader pictures. What is evident is that if we are to investigate complex ecosystem processes by either route, we should do so in such a way as to maximise relevance and to minimise the number of confounding factors. With this requirement in mind some of the more and less desirable features of 'microcosm' and 'field' approaches to the question of mycorrhizal function in ecosystems are considered below, and summarised in Table 1.1.

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